REPRODUCTIVE PATTERNS IN KING EIDERS

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REPRODUCTIVE PATTERNS IN KING EIDERS

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ABSTRACT

Mammalian predation, avian predation, female body condition and food availability on the breeding ground are likely the main factors influencing nesting success in tundra-nesting waterfowl. These driving factors are mediated by the primary life history characteristics; incubation behavior, female body size, nesting associations, and nest site selection. I created a conceptual model illustrating how these factors are inter-related and how they impact nest success through a variety of pathways to better understand the evolution of a species' nesting strategy and patterns observed in the field. The importance of the driving factors likely varies between sites and with the species nesting strategy. Given the conceptual model, I predicted the difference in life history characteristics and nesting success at two sites that vary in any of the four driving factors. I tested the model and associated predictions using King Eider females (*Somateria spectabilis)* breeding on Alaska's coastal plain by comparing selective forces influencing nesting strategies at two sites, Teshekpuk and Kuparuk, between 2002 and 2006. King Eiders fit the model with some modifications to the mediating pathways. Site differences were found in many of the reproductive parameters which matched the prediction of more available forage at Kuparuk than at Teshekpuk. No differences in either avian or mammalian predation pressure were evident between sites. Eiders at Kuparuk had higher nest survival and incubation constancy than at Teshekpuk. Body mass and nest selection were similar between sites. Although questions concerning the nesting strategies of King Eider remain, I feel that this was a valid approach to identifying selective forces impacting nesting strategies and applicable to tundra nesting waterfowl in general.

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PREFACE

This dissertation is written in five separate chapters that are each formatted for a specific journal. Chapter 2 is formatted for submission to *The Condor*, Chapter 3 is published in *Journal of Avian Biology*, Chapters 4 and 5 are published in *Journal of Wildlife Management*, and Chapter 6 is formatted for submission to *Journal of Avian Biology*. Although this thesis is single authored, co-authors are included for each individual manuscript. The 'we' in each chapter therefore refers to the multiple authors listed, but I alone take responsibility for any errors.

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Olak, at the Teshekpuk study site, logistical support, advice, and so much more. I wish he could have spent more time at Olak as I learned so much while he was in camp. I would like to thank all the people who helped with field work over the five years of the study; Yumiko Uchiro, Qiayaan Opie, Rita Frantz, Bonnie Rogers, Amanda Prevel, Miranda Wright, Keith Brady, Chris Latty, Torsten Bentzen, Kim Hanisch, Lori Guildehouse, Alexandra Hoffmann, Laura Phillips, and Steffen Oppel. They wore out many a wader for this project.

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1. INTRODUCTION

The lifetime reproductive success of female waterfowl depends, in part, upon successfully incubating a clutch and surviving to nest again. Any adaptations that serve to increase nest success, even slightly, will have a selective value (Ricklefs 1984), although negative trade-offs between life history traits could influence net selection values. Predators are often thought to be the most important selective force affecting nest success (Ricklefs 1969, Martin 1995), resulting in the evolution of a variety of strategies related to nest protection. However, options for avoiding predation are constrained by species specific life history characteristics in conjunction with available habitat. Arctic tundra-nesting waterfowl face a short breeding season, variable spring weather, little cover, and cool temperatures. In short, these are very energetically demanding conditions, possibly exerting an equally strong selective force on nesting strategies as predation.

Mammalian predation, avian predation, female spring body condition and breeding ground food availability are likely the main extrinsic factors influencing nesting success in tundra-nesting waterfowl. The effects of these four primary driving factors are mediated by four primary life history characteristics; incubation behavior, female body size, nesting associations, and nest site selection. Untangling the selective value of each of these factors is vital to understanding the evolution of a species' nesting strategy and in understanding patterns observed in the field. I developed a conceptual model (Fig. 1.1) that illustrates how these factors may be inter-related and how they likely impact nest success through a variety of potential pathways. In this conceptual model the response variable is nesting success. The arrows indicate what should be measureable

relationships. In all but one case, the effects of environmental drivers are modified by life history characteristics. Extrinsic effects are altered by life history characteristics, which is a logical outcome of natural selection for increased survival or reproductive success. Therefore, validating the model and measuring the associated relationships can yield clues about selection pressures that have shaped life history characteristics of King Eiders. The overall goal of this dissertation was to measure a variety of these hypothesized relationships and validate the conceptual model. Towards that goal, I developed lists of expected outcomes from this model given various patterns of variation in extrinsic factors. I replicated my study across 2 sites such that I was likely to encounter a range of environmental variation and thereby measure the response of nesting King Eiders to such variation. While two sites obviously represent minimal replication, it should allow broad scale assessment of relationships and allow me to validate or modify the conceptual model. Below I describe the hypothesized relationships and predict the direction of expected responses based on previously published studies.

The primary predators of tundra-nesting waterfowl eggs fall into two categories, avian (gulls [*Larus* spp.], jaegers [*Stercorarius* spp.], and ravens [*Corvus corax*]) and mammalian (Arctic fox [*Alopex lagopus*]; Larson 1960). Adaptations to avoid predation likely vary between types of predators. Incubating eiders, among the largest ducks, are unable to defend their nests from foxes (Lamothe 1973, Reed et al. 2007) and do not feign injury to draw potential predators from the nest (Larson 1960). Therefore, fox predation probability influences nest success directly. Areas with high fox predation are likely to have lower waterfowl nest survival, unless abundant alternative prey is

available. Eiders have been known to successfully deter predation attempts by gulls (Kellett and Alisauskas 1997) and jaegers (Blomqvist and Elander 1988) but most avian depredation events occur during periods when the incubating female is absent from the nest (Swennen et al. 1993, Reed et al. 2007). Therefore, the total number of nests lost to avian predation is a function of body condition and forage availability as it relates to the female's ability to maintain high constancy and may result in increased mass loss as foraging bouts are decreased.

Larson (1960) argued that two main evolutionary strategies are used by arctic tundra-nesting birds that have a limited ability to defend their nests, secluded nesting (success is increased through inaccessibility of nest location) or concealed nesting (success is increased through concealed nest location and behavior). In most waterfowl the main option for secluded breeding is to nest on islands as many mammalian predators seem adverse to crossing water. High fox predation pressure may cause waterfowl to select secluded nests which may, in turn, lead to improved nest survival. However, this strategy does not provide protection from avian predators, such as gulls and jaegers. Concealed breeders may have some degree of protection from both avian and mammalian egg predators. The concealed breeding strategy relies on the nest and hen being camouflaged to some degree, usually by the vegetation around the nest. Avian predation probability may influence females to select more concealed nests which may lead to higher success for those nests. Hens also use behavioral strategies for concealment, including spacing of nests and choices in number and length of recesses taken during

incubation. Although waterfowl typically cover their eggs when they take a recess (Afton and Paulus 1992), the activity of moving to and from the nest may attract predators.

Waterfowl may potentially gain protection from both avian and mammalian predators through associations with aggressive avian nest defenders (Giroux 1981, Blomqvist and Elander 1988, Kellett and Alisauskas 1997), that take advantage of the defensive behavior of these species towards shared predators. The adaptive significance of nesting associations by waterfowl is still unclear since many of these aggressive nest defenders (i.e., gulls, jaegers) are also significant predators of waterfowl eggs and young. Some researchers believe these associations to be advantageous (Giroux 1981, Blomqvist and Elander 1988, Kellett and Alisauskas 1997), while others consider them to be 'ecological traps' (Dwernychuk and Boag 1972), where waterfowl may produce numerous young that are subsequently eaten by neighboring gulls. If these associated aggressive nest defenders can deter mammalian predators and if waterfowl can avoid avian predation, then there may be a benefit to nesting associations. Nesting associations may be more prevalent or more beneficial when there is abundant alternative prey (Bêty et al. 2001). This is at least partly due to the fact that the associates may only nest when there is an abundance of prey (Bêty et al. 2001), however, the association may also be more beneficial if predators are not largely reliant on waterfowl eggs as a food source. Females nesting in association with avian predators may increase incubation constancy to avoid predation by the associates.

Waterfowl rely on breeding ground forage to a varying degree for egg formation and maintenance needs during incubation, and both breeding ground food availability and

body reserves garnered off the breeding grounds (spring body condition) could influence annual reproductive outcome (Fig. 1.1). Criscuolo et al. (2002) showed that female common eider (*Somateria mollissima*) body stores generally allow them to complete incubation within a very limited safety margin and that females will decrease constancy and begin feeding if this critical body mass is reached. Therefore, poor spring body condition may lead to long foraging bouts during incubation and lower incubation constancy as females attempt to maintain body mass above some critical threshold. This may lead to decreased nest survival if avian predators are prevalent. Similarly, low breeding ground forage availability may lead directly to decreased incubation constancy if foraging bouts are longer. Again, this could lead to lower nest survival. Alternatively, females in poor spring body condition may maintain high constancy at the cost of increased mass loss. This could lead to increased nest abandonment if females deplete their fat reserves during incubation, or to abandonment or loss of the brood, but may benefit the female if she can avoid predation and maintain body mass above a critical threshold (Fig. 1.1). Criscuolo (et al. 2002) found that while females were able to limit mass loss while continuing incubation, some females did eventually abandon their clutches. Spring body condition and forage availability effect incubation constancy, weight loss, and nest success similarly, making it difficult to separate the two factors simply through observation of patterns in the field.

Degree of reliance on body reserves is generally correlated with female body size and is positively related to incubation constancy (Afton and Paulus 1992). The ability to maintain high incubation constancy may be an important factor in determining nest

success if the majority of egg depredation occurs during incubation recesses (Swennen et al. 1993). Females may time incubation recesses to minimize exposure to predation (Afton 1980, Swennen et al. 1993), to take advantage of the warmest part of the day to reduce cooling of eggs (Flint and Grand 1999, MacCluskie and Sedinger 1999, Quakenbush et al. 2004), or simply as metabolic costs demand. Females in areas with poor forage availability are likely to decrease incubation constancy in an effort to meet some optimal rate of mass loss during incubation (Criscuolo et al. 2002). This in turn could lead to lower nest success. This relationship is likely exacerbated if the female arrives at the breeding grounds in poor condition; she will need to feed more during incubation to maintain adequate body condition. Females relying on endogenous reserves for maintenance needs during incubation are likely to choose nest sites and time recesses to maximize predator avoidance while those relying on exogenous resources also need to consider food availability.

The importance of these four driving factors likely varies between sites, or years, and the nesting strategy of the species in question. Given the conceptual model (Fig. 1.1), I predicted the difference in the mediating life history characteristics and nesting success when compared between two sites, or two years, which may vary in predation pressure, spring female body condition, and breeding ground food availability (Tables 1.1-1.4). The tables hinges on a number of key predictions: 1) females will have higher incubation constancy if higher food availability allows for efficient foraging or if better spring body condition allows for a greater weight loss, 2) higher incubation constancy will lead to higher nest survival if mammalian predation pressure is equal, 3) females will maintain

higher incubation constancy when avian predation pressure is higher, possibly counteracting increased predation pressure, 4) females will choose and benefit from concealment in the presence of avian predation pressure, 5) females will choose and benefit from seclusion in the presence of mammalian predation pressure, and 6) females will choose nesting associates in the presence of higher avian or mammalian predation pressure.

The predictions (Tables 1.1-1.4) have a number of inherent assumptions which should be evaluated for individual studies. First, I assume available habitat is constant between sites or years, in aspects other than food availability. For example, the protection provided by a secluded nest site should not vary between sites if predation pressure does not vary. I assume that habitat is similar on islands and mainland sites so that the main reason to choose an island is to avoid mammalian predation. Additionally, I assume that islands provide some protection. I assume that there is some optimal rate of mass loss that female waterfowl attempt to maintain during incubation so as to end incubation in adequate body condition and that incubation constancy can be modified to meet this rate. Females may decrease foraging bouts (increasing constancy) either because high available forage allows for efficient foraging, because they arrived in better body condition and have more fat reserves to burn, or in response to avian predation pressure. The latter should be coupled with increased weight loss. The conceptual model (Fig. 1.1) and associated predictions (Tables 1.1-1.4) are designed to aid in determining the difference in selective factors between two sites and can be modified for individual situations. For example, if females are known to fast during incubation then variability in

available forage is unlikely to influence reproductive patterns and can be eliminated from the table. Similarly, if it is possible to show that females arrive at the breeding grounds in the same body condition, the predictions for variation in body condition can be eliminated.

It is the goal of my dissertation to validate or reject specific components of this model by testing the various predictions using female King Eiders (*S. spectabilis)* breeding on Alaska's coastal plain. I compare selective forces influencing the nesting strategies of King Eiders at two sites on Alaska's coastal plain between 2002 and 2006. King Eiders are near the extremes of the waterfowl continuum in terms of severity of climate and reliance on nutrient reserves during incubation (Kellett 1999). Although females feed during egg laying and eggs are composed largely of nutrients obtained on the breeding grounds (Oppel 2008), they likely rely heavily on endogenous reserves during incubation (Kellett 1999, Lawson 2006). Thus, both endogenous reserves and breeding ground resources may be important to nest success. In any given year, most King Eider nests are lost to predation, and females will occasionally abandon a nesting attempt. Although King Eiders have declined significantly over the past 20 years (Suydam et al. 2000), little is known about their nesting strategies. Given that much of their nesting habitat in Alaska is open for oil and gas extraction (Bureau of Land Management 1998, Bureau of Land Management 2004), it is vital for future management to mitigate of the impacts of development that we understand what selective forces are influencing the reproductive patterns that we observe in the field.

Literature cited

Afton, A. D. 1980. Factors affecting incubation rhythms of Northern Shovelers. Condor 82: 132-137.

Afton, A. D., and S. L. Paulus. 1992. Incubation and brood care. Pages 62-108 *in*: B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu. editors. Ecology and management of breeding waterfowl. University Minnesota Press, Minneapolis.

Bêty, J., G. Gauthier, J. –F. Giroux, and E. Korpimäki. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. Oikos 93:388-400.

Blomqvist, S., and M. Elander. 1988. King eider (*Somateria spectabilis*) nesting in association with long- Dwernychuk, L.W., and D. A. Boag. 1972. How vegetative cover protects duck nests from egg-eating birds. Journal of Wildlife Management 36: 955-958.

Bureau of Land Management. 1998. Record of decision for the Northeast Petroleum Reserve-Alaska integrated activity plan/environmental impact statement. U.S. Department of Interior, Bureau of Land Management, Anchorage, Alaska, USA.

Bureau of Land Management. 2004. Record of decision for the Northwest National Petroleum Reserve-Alaska integrated activity plan/environmental impact statement. U.S. Department of Interior, Bureau of Land Management, Anchorage, Alaska, USA.

Criscuolo, F., Gabrielsen, G. W., Gendner, J. –P. and Le Maho, Y. 2002. Body mass regulation during incubation in female common eiders *Somateria mollissima.* Journal of Avian Biology 33:83-88.

Dwernychuk, L.W., and D. A. Boag. 1972. How vegetative cover protects duck nests from egg-eating birds. Journal of Wildlife Management 36:955-958.

Flint, P. L., and J. B. Grand. 1999. Incubation behavior of Spectacled Eiders on the Yukon-Kukokwim Delta, Alaska. Condor 101: 413-416.

Giroux, J. 1981. Ducks nesting in association with Canada geese. Journal of Wildlife Management 45: 778-782.

Kellett, D. K. 1999. Causes and consequences of variation in nest success of king eiders (*Somateria spectabilis*) at Karrak Lake, Northwest Territories. Thesis, University of Saskatchewan, Saskatoon, Canada.

Kellett, D. K., and R. T. Alisauskas. 1997. Breeding biology of king eiders nesting on Karrak Lake, Northwest Territories. Arctic 50: 47-54.

Lamothe, P. 1973. Biology of the king eider (*Somateria spectabilis*) in a freshwater breeding area on Bathurst Island, N.W.T. Thesis, University of Alberta, Edmonton, Canada.

Larson, S. 1960. On the influence of the arctic fox *Alopex lagopus* on the distribution of arctic birds. Oikos 11: 276-305.

Lawson, S. 2006. Comparative reproductive strategies between long-tailed ducks and king eiders at Karrak Lake, Nunavut: use of energy resources during the nesting season. Thesis, University of Saskatchewan, Saskatoon, Canada.

MacCluskie, M., and J. Sedinger. 1999. Incubation behavior of Northern Shovelers in the subarctic: A contrast to the prairies. Condor 101:417-421.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. Ecological Monographs 65: 101-127.

Oppel, S. 2008. King eider migration and seasonal interactions at the individual level. Ph.D. Dissertation, University of Alaska Fairbanks, Fairbanks, USA.

Quakenbush, L., R. Suydam, T. Obritschkewitsch, and M. Deering. 2004. Breeding biology of Steller's eiders (*Polysticta stelleri*) near Barrow, Alaska, 1991-99. Arctic 57: 166-182.

Reed, J. A., D. L. Lacroix, and P. L. Flint. 2007. Depredation of Common Eider, Somateria mollissima, nests on a central Beaufort Sea barrier island: a case where no one wins. Canadian Field-Naturalist 121: 308-312.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9: 1-48.

Ricklefs, R. E. 1984. Variation in the size and composition of eggs of the European starling. Condor 86: 1-6.

Swennen, C., J. C. H. Ursem, and P. Duiven. 1993. Determinate laying and egg attendance in common eiders. Ornis Scandinavica 24: 48-52.

Suydam, R. S., D. L. Dickson, J. B. Fadely, and L. T. Quakenbush. 2000. Population declines of king and common eiders of the Beaufort Sea. Condor 102: 219-222.

Table 1.1. Predicted difference in reproductive parameters of tundra-nesting waterfowl with varying available forage and female body condition on arrival at the breeding grounds relative to a nesting area with equal fox and avian predation pressure.

	Habitat		
	Equal available forage	**More available forage**	**Parameters**
Female condition on arrival equal	Equal	Higher	Incubation constancy
	Equal	Higher	Nest success
	Choose similar nests	Choose similar nests	Seclusion
	Choose similar nests	Choose similar nests	Concealment
	Similar between sites	Similar between sites	Nesting associations
	Equal	Equal	Weight loss
Female condition on arrival higher	Higher	Higher	Incubation constancy
	Higher	Higher	Nest success
	Choose similar nests	Choose similar nests	Seclusion
	Choose similar nests	Choose similar nests	Concealment
	Similar between sites	Similar between sites	Nesting associations
	Equal	Equal or lower	Weight loss

Table 1.2. Predicted differences in reproductive parameters of tundra-nesting waterfowl with varying available forage and female body condition on arrival at the breeding grounds relative to a nesting area with lower avian predation pressure but equal fox predation pressure.

	Habitat		
	Equal available forage	**More available forage**	**Parameters**
Female condition on arrival equal	Higher or equal	Higher	Incubation constancy
	Equal or lower	Equal	Nest success
	Choose similar nests	Choose similar nests	Seclusion
	Choose and benefit from concealment	Choose and benefit from concealment	Concealment
	Fewer associations	Fewer associations	Nesting associations
	Higher or equal	Equal	Weight loss
Female condition on arrival higher	Higher	Higher	Incubation constancy
	Equal	Equal	Nest success
	Choose similar nests	Choose similar nests	Seclusion
	Choose and benefit from concealment	Choose and benefit from concealment	Concealment
	Fewer associations	Fewer associations	Nesting associations
	Equal	Equal	Weight loss

Table 1.3. Predicted differences in reproductive parameters of tundra-nesting waterfowl with varying available forage and female body condition on arrival at the breeding grounds relative to a nesting area with equal avian predation pressure and lower fox predation pressure.

	Habitat		
	Equal available forage	**More available forage**	**Parameters**
Female condition on arrival equal	Equal	Higher	Incubation constancy
	Lower	Lower	Nest success
	Choose and benefit from seclusion	Choose and benefit from seclusion	Seclusion
	Choose similar nests	Choose similar nests	Concealment
	Fewer associations	Fewer associations	Nesting associations
	Equal	Equal	Weight loss
Female condition on arrival higher	Higher	Higher	Incubation constancy
	Lower	Lower	Nest success
	Choose and benefit from seclusion	Choose and benefit from seclusion	Seclusion
	Choose similar nests	Choose similar nests	Concealment
	Fewer associations	Fewer associations	Nesting associations
	Equal	Equal or lower	Weight loss

Table 1.4. Predicted differences in reproductive parameters of tundra-nesting waterfowl with varying available forage and female body condition on arrival at the breeding grounds relative to a nesting area with lower avian predation pressure and lower fox predation pressure.

	Habitat		
	Equal available forage	**More available forage**	**Parameters**
Female condition on arrival equal	Higher or equal	Higher	Incubation constancy
	Lower	Lower	Nest success
	Choose and benefit from seclusion	Choose and benefit from seclusion	Seclusion
	Choose and benefit from concealment	Choose and benefit from concealment	Concealment
	Fewer associations	Fewer associations	Nesting associations
	Higher or equal	Equal	Weight loss
Female condition on arrival higher	Higher	Higher	Incubation constancy
	Lower	Lower	Nest success
	Choose and benefit from seclusion	Choose and benefit from seclusion	Seclusion
	Choose and benefit from concealment	Choose and benefit from concealment	Concealment
	Fewer associations	Fewer associations	Nesting associations
	Equal	Equal or lower	Weight loss

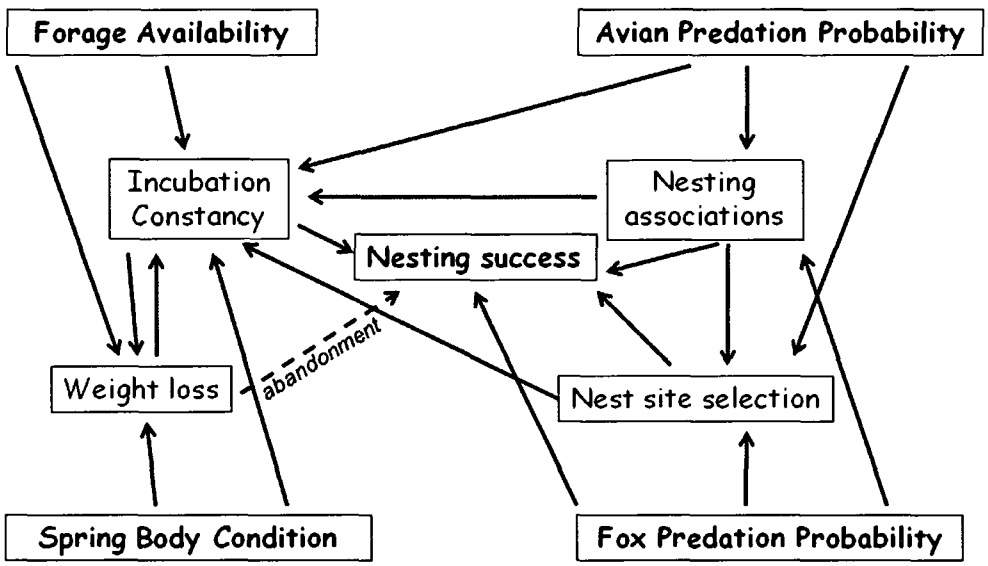

Figure 1.1. Conceptual model of the major driving factors and mediating life history characteristics influencing nest survival for tundra-nesting waterfowl.

2. INCUBATION BEHAVIOR OF KING EIDERS ON THE COASTAL PLAIN OF NORTHERN ALASKA[1]

2.1. Abstract

Incubating birds must balance their energetic demands during incubation with the needs of the developing embryos. Reduced nest attendance rates can lead to lower egg viability, increased risk of egg depredation, and increased incubation period. We examined patterns of nest attendance of King Eiders (*Somateria spectabilis)* at two sites, Teshekpuk and Kuparuk, in northern Alaska (2002-2005) in relation to nesting habitat, daily temperature, and to the female's endogenous reserves, to explore factors controlling incubation behavior. King Eiders had very high incubation constancy, with Kuparuk (99%) slightly higher than Teshekpuk (97%). Females took an average of 0.60 recesses day^{-1} at both sites, with an average length of 22.7 minutes at Kuparuk and 35.7 minutes at Teshekpuk. Female body mass on arrival to the breeding grounds, and at the end of incubation, did not vary between sites or among years. Female body mass and minimum daily temperatures were positively correlated with overall and daily incubation constancy, respectively. The relationship between body mass, temperature, and increased incubation constancy, coupled with similar mass loss between sites, implied that incubation behavior is functionally driven by local foraging conditions and metabolic costs. It appears King Eiders attempt to achieve an optimal rate of mass loss through modification of their

[1]Bentzen, R. L., A. N. Powell, L. M. Phillips, and R. S. Suydam. 2008. Incubation behavior of king eiders on the coastal plain of northern Alaska. Prepared for submission in Condor.

incubation behavior in response to endogenous nutrient reserves available for maintenance needs and environmental conditions.

2.2. Introduction

Incubating birds face trade-offs between maintenance of egg viability, loss of energy reserves, and risk of predation (Thompson and Raveling 1987, Afton and Paulus 1992). Females can benefit from increased incubation constancy through increased egg-hatchability, shortened incubation periods (Aldrich and Raveling 1983, Zicus et al. 1995), and decreased predation (Swennen et al. 1993), at the expense of female body condition and potential predation risk (Afton and Paulus 1992). Afton and Paulus (1992) asserted that incubation behavior is strongly correlated with body size; larger birds are able to accumulate more endogenous reserves and therefore can maintain higher incubation constancy (i.e. the percentage of time spent incubating eggs). Reliance on endogenous reserves is manifested by mass lost by the female over the incubation period; it has been suggested that females can modify their mass loss by increasing recess time (Mallory and Weatherhead 1993) if reserves are used during incubation and forage is available. This is functionally a "top-down argument" in that it implies that an incubating female bases her foraging decisions simply on energetic demands based on endogenous reserves and predator avoidance. Alternatively, foraging decisions by incubating females may be under "bottom-up" control as it is related to variation in food availability (Gatti 1983, Harvey et al. 1988, Flint and Grand 1999).

Arctic-nesting waterfowl contend with variable and cold spring weather, little cover, and low food availability (Ankney and MacInnes 1978, Gloutney et al. 2000) and often rely heavily on endogenous reserves. The importance of endogenous reserves for successful incubation has been demonstrated in arctic-nesting Lesser Snow Geese (*Chen caerulescens*; Ankney and MacInnes 1978) and coastal-nesting Common Eiders (*Somateria mollissima*; Korschgen 1977). The ability to maintain high incubation constancy may be an important factor in determining nest success if the majority of egg depredation occurs during incubation recesses (Swennen et al. 1993). Females may time incubation recesses to minimize exposure to predation (Afton 1980, Swennen et al. 1993). Alternately, females may time breaks to take advantage of the warmest part of the day to reduce cooling of eggs, although it is often when avian predators are most active (Flint and Grand 1999, MacCluskie and Sedinger 1999, Quakenbush et al. 2004).

King Eiders (*Somateria spectabilis)* breed at the extremes of the waterfowl continuum in terms of severity of climate and predicted reliance on nutrient reserves (Kellett 1999). However, they appear to employ a partial-income incubation and egg production strategy in Alaska, using both endogenous and exogenous energy resources to a varying degree (Bentzen et al. 2008a, Oppel 2008). Feeding during incubation is likely a mechanism to slow the rate of mass loss, not prevent it entirely, and may allow females to complete incubation within a safety margin for body mass (Mallory and Weatherhead 1993, Criscuolo et al. 2002). Analysis of fat metabolites at two sites in northern Alaska, Teshekpuk and Kuparuk, indicated that King Eiders may differ in nutritional strategies between population segments as females at the cooler site experienced both higher food

intake and higher metabolic costs (Bentzen et al. 2008a). With this study we further investigate the incubation strategies of King Eiders nesting at Teshekpuk and Kuparuk, Alaska. The goals were twofold. First, we described incubation behavior in terms of incubation constancy, recess frequency, and recess length, and examined patterns in overall incubation constancy between sites, years, and island/mainland nest location. Second, in a correlative study, we investigated factors controlling incubation behavior; specifically, we examined the importance of 1) daily minimum and maximum temperatures, and 2) endogenous reserves at arrival and during the incubation period on incubation behavior.

2.3. Methods

2.3.1 Study area and nest searches

We studied King Eiders nesting at two sites on the North Slope of Alaska, one near Teshekpuk Lake (153°07'W, 70°25'N) and another within the Kuparuk oilfields (149°41'W, 70°27'N) from 2002-2005. The Teshekpuk study site was approximately 10 km inland from the southeast shore of Teshekpuk Lake and to date has experienced minimal human impact. The Kuparuk study site was in an area between the Colville and Kuparuk river deltas developed for oil production.

We systematically searched wetland basins on foot for King Eider nests, beginning in mid-June at both sites. We searched a larger area at Kuparuk (Teshekpuk ~1000 ha; Kuparuk ~1500 ha) because of road access at that site. We marked nests with a tongue depressor placed 1 m from the nest in vegetation to conceal them from potential

nest predators, and recorded latitude and longitude using a hand-held Global Positioning System (GPS) unit. We calculated nest-initiation dates either by backdating from known laying dates or from estimated incubation stages by candling eggs (Weller 1956), assuming a laying interval of one egg per day and an incubation length of 23 days (Lamothe 1973). We monitored all nests weekly. We designated a successful hatch by the presence of either eggshells with detached membranes (Girard 1939) or ducklings. If there were eggshells with no membranes, or if the entire egg was absent, we considered the nest depredated. Nest sites were classified as an island or mainland at hatch; we defined islands as sites where we had to cross any depth and distance of water to reach them.

2.3.2. Incubation constancy

We placed data loggers (HOBO-TEMP, Onset Computer Corporation) opportunistically in nests at Teshekpuk and Kuparuk, 2002-2005 (n = 66), and programmed them to record nest temperature every 2 min. We used blown chicken eggs, dyed an olive green and attached to a bolt, to hold the thermistor probes (see Quakenbush et al. 2004). The bolt was driven into the ground under the nest, anchoring the probe and dummy egg in the nest. This allowed for a quick response to any change in temperature because the probe had only an eggshell between it and the incubating female. The duration that the HOBO egg recorded temperature at each nest was variable because most (66%) nest attempts failed, at which point the HOBO egg was moved to a new nest. We attempted to limit disturbance; only 15 of the 66 nests were flushed after the initial nest visit. Finally, we placed a Sentinel Video Camera Surveillance System (Sandpiper Technologies, Inc.®) at

one nest at Kuparuk in 2003 in order to validate the HOBO temperature data. The video system consisted of a weatherproof miniature video camera with six infrared light-emitting diodes (940 nm-wavelength not visible to vertebrates) attached via a cable to a time-lapse videocassette recorder (Panasonic AG1070) housed in a weatherproof case powered by a 12-volt deep-cycle marine battery. The VCR and battery were placed approximately 25 m from the nest. We set the time-lapse VCR to record 24 h of video on standard T 160 VHS videotapes (5 frames/second).

We did not use any temperature records that occurred during egg laying. Temperature streams shorter than one day were excluded, as were records from nests (n = 7) where temperatures were impossible to interpret. This was likely due to the HOBO egg being placed too close to the edge of nest and being uncovered at times, despite the female actually being present. We did not use temperature records from any days in which the female was flushed from the nest due to our activities.

We defined an "incubation recess" as $\geq 1.5°$ C drop in temperature between successive temperature measurements followed by two successive $\geq 0.5°$ C drops. Therefore, as temperature was recorded every 2 min, we can only detect recesses longer than 6 min. Our classification was validated both by data from the female at Kuparuk that had a HOBO logger in her nest and was video-recorded continuously, and by temperature data for females (n = 12) that were flushed or absent during nest checks while the HOBO logger was recording. Our criteria avoided classifying movements on the nest as recesses, and correctly identified all but one of the flushes caused by our nest checks.

We defined incubation constancy as the percentage of time the female was on her nest over the period of days for which we had data. Daily incubation constancy was defined as incubation constancy during a 24-h period beginning at midnight. Recess frequency was the average number of breaks taken per day over the period in which the temperature was recorded in the nest.

2.3.3. Weather

We obtained minimum and maximum daily temperature records for Kuparuk (70°19'N, 149°35'W) online from the National Climatic Data Center (2007). An Onset HOBO Weather Station (Onset Computer Corporation) was installed at Teshekpuk in 2002-2004. Temperature was recorded with a HOBO-TEMP at Teshekpuk in 2005 (Onset Computer Corporation).

2.3.4. Body condition

We trapped female King Eiders using mist nets upon their arrival (mid June) to the breeding grounds at Kuparuk (2002-2005) and Teshekpuk (2004-2005). We trapped a separate sample of females on the nest using a drop or bow net close to hatch (>18 days after initiation of incubation) at Kuparuk (2002, 2003, and 2005) and Teshekpuk (2005). Of the females trapped late in incubation ($n = 44$) for body mass measurements, only six were birds with HOBOs in the nest. A subset of the HOBO birds ($n = 16$, including the above 6) were trapped during mid- to late-incubation (8-22 days after initiation) at both sites in 2005 to determine the effects of body mass on incubation constancy. We banded (United States Fish and Wildlife Service aluminum bands) all captured birds, and took

morphometric and mass measurements. All aspects of the field work were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (05-29-King Eider).

2.3.5. Statistical analysis

We used general linear models to evaluate factors influencing overall incubation constancy using 32 *a priori* candidate models involving combinations of the following variables: site, year, island/mainland nest location, and all possible interactions. We examined variation in daily incubation constancy in relation to day of incubation using analysis of covariance with individuals as a factor (n = 44 females) and day of incubation as a covariate. Having established some gross patterns in incubation constancy, we evaluated a separate set of candidate models investigating factors influencing daily incubation constancy, including 15 *a priori* models with combinations of the variables minimum daily temperature, maximum daily temperature, site, and day of incubation. We used Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002) to select the best approximating models with both candidate sets. We model-averaged parameter estimates and associated variances from the 95% confidence set of candidate models (Burnham and Anderson 2002). We used arcsine square root-transformations for daily and total incubation constancy to improve normality of the data.

We used Rayleigh's test for circular uniformity (Zar 1999) to test if recesses were equally likely to occur throughout a 24-h day (Alaska Standard Time). All eight year-sites conformed to a von Mises distribution (Watson's $U^2 < 0.08$, $P > 0.05$). However, the

concentrations were low and unequal among groups so we used the nonparametric Mardia-Watson-Wheeler test for more than two samples (Zar 1999) to determine if the distribution of recess times differed between sites and years. These analyses were conducted using Oriana (Kovach Computing Services 2005).

We compared body mass of females upon arrival to the breeding grounds between sites and years using a two-way analysis of variance (ANOVA), and body mass of females late in incubation (>18 days incubation) between sites and years using a second two-way ANOVA. We examined variation in incubation constancy in relation to body mass of females at the time of trapping, controlled for nest age at trapping, using linear regression. Values are reported as means ± SE (or circular SD). Analyses were conducted using SAS (SAS Institute 1990). We considered results significant at $\alpha < 0.05$.

2.4. Results

2.4.1 Incubation constancy

Incubation constancy was high, averaging 99% at Kuparuk and 97% at Teshekpuk. Mean recess length ranged from 21.5 - 23.7 min at Kuparuk, and from 28.5 - 51.2 min at Teshekpuk. Mean recess frequency ranged from 0.43 - 0.71 day^{-1} at Kuparuk and 0.44 - 0.65 day^{-1} at Teshekpuk between years (Table 2.1).

The top three models of the candidate model set examining factors that influence overall incubation constancy were similar in terms of AIC_c and included the parameters site and year (Table 2.2). Model-averaged parameter estimates (effect sizes, θ) from the

top models indicated that incubation constancy was higher at Kuparuk than Teshekpuk (θ_{site} = 0.03, 95% CI 0.00, 0.06), and higher in 2002 (θ_{2002} = 0.03, 95% CI 0.00, 0.07) and 2004 at Teshekpuk (θ_{2004} = 0.04, 95% CI 0.00, 0.08) relative to 2005. Incubation constancy did not differ between island/mainland nest sites (θ_{island} = 0.003, 95% CI -0.01, 0.02) or 2003 relative to 2005 (θ_{2003} = 0.02, 95% CI -0.02, 0.05). The difference in incubation constancy between the sites was largely driven by the length of the recess rather than the frequency of recesses. The relationship between daily incubation constancy and day of incubation varied among females ($F_{43,364}$ = 1.5, P = 0.03).

The top five models of the candidate model set examining the factors influencing daily incubation constancy were also similar and included the parameters minimum daily temperature, maximum daily temperature, nest age, and site (Table 2.3). The effect of minimum daily temperature appeared in all top models. Model-averaged parameter estimates (regression coefficients, β) from the top models indicated that daily incubation constancy increased with minimum daily temperature (β_{min} = 0.006, 95% CI 0.003, 0.01) but did not differ from zero for the other covariates. Minimum daily temperature was on average 1.5° C higher at Teshekpuk than Kuparuk, controlling for day of the season ($F_{2,367}$ = 55.8, P < 0.001). Maximum daily temperature was also higher at Teshekpuk (2.7° C; $F_{2,361}$ = 45.5, P < 0.001). The effect of temperature on daily incubation constancy did not vary with site ($\beta_{min*site}$ = 0.002, 95% CI 0.008, -0.004)

Mean recess start time varied between 13:26 and 14:40 h among years and was different from a uniform distribution at both sites from 2002-2004 (Z > 3.6, P < 0.03), but

did not differ from the uniform distribution at either site in 2005 ($Z < 1.6$, $P > 0.2$). The distribution of recess start times at Kuparuk in 2003 (13:58 h ± 65.4°) varied significantly from Kuparuk 2005 (14:38 h ± 109°), Teshekpuk 2002 (13:39 hours ± 94°), Teshekpuk 2004 (13:26 h ± 107°), and Teshekpuk 2005 (14:40 h ± 118°; $W > 6.1$, $P < 0.05$). The remaining pairwise comparisons did not differ ($W < 3.3$, $P > 0.05$). Island nests did not have the same distribution of recess times as those on the mainland ($W = 15.7$, $P < 0.001$). Recess start time averaged 13:33 h (± 80.9°) on islands and 14:57 h (± 107°) on mainland sites.

2.4.2 Body condition

We trapped females slightly earlier at Teshekpuk (13-16 June 2004; 11-15 June 2005) than Kuparuk (18-19 June 2004; 17-21 June 2005) in both years. Female body mass at arrival did not differ between sites ($F_{1,27} = 1.1$, $P = 0.31$) or among years ($F_{3,27} = 0.9$, $P = 0.47$). Body mass late in incubation (>18 days) did not differ between sites ($F_{1,41} = 0.7$, $P = 0.42$) or years ($F_{2,41} = 0.3$, $P = 0.74$; Table 2.4). Females at Teshekpuk were 34.9% lighter during late incubation than those trapped upon arrival in 2005. Females at Kuparuk lost slightly less mass, 26.3% in 2002, 33.4% in 2003 and 31.1% in 2005. Incubation constancy was positively correlated with body mass at trapping, controlled for nest age ($F_{2,13} = 13.8$, $P < 0.001$, $r^2 = 0.68$).

2.5. Discussion

King Eiders exhibited high incubation constancy at both sites in all years. They were close in incubation constancy to Common Eiders which are among the most extreme of

waterfowl in that they loose up to 42% of their body mass during incubation (Korschgen 1977, Parker and Holm 1990) and have an incubation constancy of 99.5% (*S. m. mollissima;* Bolduc and Guillemette 2003). Female Common Eiders are believed to fast during incubation, providing a plausible explanation for this substantial loss in body mass, taking breaks mainly to drink and preen (Bolduc and Guillemette 2003). King Eiders feed to some extent during incubation (Bentzen et al. 2008a), losing relatively less mass during incubation (31%, this study; 30%, Kellett and Alisauskas 2000), while maintaining similar high incubation constancy (95-99%). However, as predicted, King Eiders appear to rely more heavily on endogenous reserves than smaller bodied sub-arctic nesting ducks which spend less time on the nest, and lose a comparatively lower proportion of body mass during the incubation period (Fig. 2.1).

Incubation attentiveness is often thought to be positively related to mass loss (Aldrich and Raveling 1983, Afton and Paulus 1992, Mallory and Weatherhead 1993); that is, individuals/populations/species that have high incubation attendance rates are expected to have comparatively higher mass loss during incubation. However, we found that although females arrived at both breeding areas and completed incubation at similar body masses, hens at Kuparuk had higher incubation constancies. As there was appreciable intake of food by incubating females (Bentzen et al. 2008a), this increased incubation constancy coupled with no change in mass loss implies that incubation behavior was functionally driven by local foraging conditions (Flint and Grand 1999, Flint 2003). It appeared that hens at Kuparuk met foraging requirements (i.e. reduced mass loss to some optimal level) with shorter incubation recesses than those at

Teshekpuk. This conclusion is supported by the finding of Bentzen et al. (2008a) indicating that females incubating at Kuparuk had higher food intake rates than those at Teshekpuk. It appeared that even for a species with very high incubation attendance such as King Eiders, incubation behavior is dictated by local forage quality.

Females exhibited lower incubation constancy in 2005 at both sites relative to the previous three years, although nest survival and initiation of laying did not vary (Bentzen et al. 2008b). This may have been due to the relatively cold, late spring in 2005, which likely increased energetic demands on laying and incubating females, potentially reduced available exogenous resources, and thus led to reduced incubation constancy. This was different than predicted under a scenario where recesses are optimized to reduce egg cooling (Afton and Paulus 1992). Under this hypothesis, females should take fewer breaks in cold years, and lose more mass during incubation. In contrast, if metabolic costs drive incubation behavior, females would be forced to spend more time off the nest foraging in a cold year but potentially lose the usual amount of mass. In our study, females spent more time off the nest at lower minimum daily temperatures, supporting the hypothesis that metabolic costs and local foraging conditions were driving incubation behavior.

Temperature variation within days may also play a role in the optimization of incubation behavior; females took recesses at roughly the same time of day between sites and among years, which could indicate some commonality that selects for recesses in the mid-afternoon. Females may save energy by taking incubation recesses during the

warmest part of the day (Flint and Grand 1999, Quakenbush et al. 2004) if they have the body reserves to wait to such a time, or potentially to avoid predation if predators are less active during this time. Female body mass may be particularly important to King Eider incubation behavior; we found that 68% of the variation in incubation constancy was explained by body mass of the female. Additionally, the relationship between daily incubation constancy and day of incubation varied significantly among females. This was likely driven by individual optimization of incubation behavior in relation to nest-site microhabitat, body condition, female experience, foraging efficiency, and predation risk (Flint and Grand 1999, MacCluskie and Sedinger 1999, Flint 2003).

In conclusion, it appears that there is an optimal rate of mass loss during incubation, and King Eiders modify their incubation behavior based on endogenous nutrient reserves available for maintenance needs and local foraging conditions to achieve this rate. We observed high incubation constancies at both sites in all years, with considerable individual variation in incubation behavior. Incubation constancy was lower at Teshekpuk, but we found no differences between sites in female body condition upon arrival to the breeding grounds or at the end of incubation. Additionally, at low ambient temperatures hens spent more time off nests, suggesting increased daily maintenance needs which were potentially ameliorated by feeding during these recesses.

2.6. Acknowledgements

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ConocoPhillips Alaska Inc., United States Geological Survey, Alaska Cooperative Fish and Wildlife Research Unit, and Sandpiper Technologies Inc. Funding from the North Slope Borough was through the National Petroleum Reserve-Alaska Impact Mitigation Program. North Slope Borough Search and Rescue provided some helicopter support. This study was endorsed by the Sea Duck Joint Venture. We thank the administrative staff at the North Slope Borough Department of Wildlife Management, ConocoPhillips Inc. Environmental Studies, and all the many field technicians. Comments by Paul Flint, Alexander Kitaysky, and Dana Thomas were greatly appreciated and improved previous versions of the manuscript. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. government.

2.7. Literature cited

Afton, A. D. 1980. Factors affecting incubation rhythms of Northern Shovelers. Condor 82:132-137.

Afton, A. D., and S. L. Paulus. 1992. Incubation and brood care, p. 62-108. *In* B. D. Batt, A. D. Afton, M. G. Anderson, C. D. Ankney, D. H. Johnson, J. A. Kadlec, and G. L. Krapu [eds.], Ecology and Management of Breeding Waterfowl. University Minnesota Press, Minneapolis, MN.

Aldrich, T. W., and D. G. Raveling. 1983. Effects of experience and body weight of incubation behavior of Canada Geese. Auk 100:670-679.

Ankney, C. D., and C. D. MacInnes. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. Auk 95:459-471.

Bentzen, R. L., Powell, A. N., Williams, T. D., and Kitaysky, A. S. 2008a. Characterizing the nutritional strategy of incubating king eiders *Somateria spectabilis* in northern Alaska. Journal of Avian Biol. 39: 683-690.

Bentzen, R. L., Powell, A. N., and Suydam, R. S. 2008b. Factors influencing nesting success of king eiders on northern Alaska's coastal plain. Journal of Wildlife Manage. 72: 1781-1789.

Bolduc, F., and M. Guillemette. 2003. Incubation constancy and mass loss in the Common Eider *Somateria mollissima*. Ibis 145:329-332.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, 2nd ed. Spring-Verlag, New York.

Criscuolo, F., Gabrielsen, G. W., Gendner, J. –P. and Le Maho, Y. 2002. Body mass regulation during incubation in female common eiders *Somateria mollissima.* Journal of Avian Biology 33:83-88.

Flint, P. L. 2003. Incubation behaviour of Greater Scaup *Aythya marila* on the Yukon-Kuskokwim Delta, Alaska. Wildfowl 54:71-79.

Flint, P.L. , and J. B. Grand. 1999. Incubation behavior of Spectacled Eiders on the Yukon-Kukokwim Delta, Alaska. Condor 101:413-416.

Gatti, R. C. 1983. Incubation weight loss in the mallard. Canadian Journal of Zoology 61:565-569.

Girard, G. L. 1939. Notes on the life history of the shoveler. Transactions of the North American Wildlife Conference 4:364-371.

Gloutney, M. L., R. T. Alisauskas, A. D. Afton, and S. M. Slattery. 2000. Foraging time and dietary intake by breeding Ross's and Lesser Snow geese. Oecologia 127:78-86.

Harvey, W. F., G. R. Hepp, and R. A. Kennamer. 1988. Body mass dynamics of wood ducks during incubation: individual variation. Canadian Journal of Zoology 67:570-574.

Kellett, D. K. 1999. Causes and consequences of variation in nest success of King Eiders (*Somateria spectabilis*) at Karrak Lake, Northwest Territories. M.Sc.thesis, University of Saskatchewan, Saskatoon, Saskatchewan.

Kellett, D. K., and R. T. Alisauskas. 2000. Body-mass dynamics of King Eiders during incubation. Auk 117:812-817.

Korschgen, C. E. 1977. Breeding stress of female eiders in Maine. Journal Wildlife Management 41:360-373.

Kovach Computing Services. 2005. Oriana Version 1. Kovach Computing Services, Anglesey, Wales.

Lamothe, P. 1973. Biology of the King Eider (*Somateria spectabilis*) in a freshwater breeding area on Bathurst Island, N.W.T. M.S. Thesis, University of Alberta, Edmonton, Alberta.

MacCluskie, M., and J. Sedinger. 1999. Incubation behavior of Northern Shovelers in the subarctic: A contrast to the prairies. Condor 101:417-421.

Mallory, M. L., and P. J. Weatherhead. 1993. Incubation rhythms and mass loss of Common Goldeneyes. Condor 95:849-859.

National Climatic Data Center [online]. 2007. Climate-radar data inventories. <http://www.ncdc.noaa.gov/oa/ncdc.html> (13 February 2007).

Oppel, S. 2008. King eider migration and seasonal interactions at the individual level. Ph.D. Dissertation, University of Alaska Fairbanks, Fairbanks, USA.

Parker, H., and H. Holm. 1990. Patterns of nutrient and energy expenditure in female Common Eider nesting in the high arctic. Auk 107:660-665.

Quakenbush, L., R. Suydam, T. Obritschkewitsch, and M. Deering. 2004. Breeding biology of Steller's Eiders (*Polysticta stelleri*) near Barrow, Alaska, 1991-99. Arctic 57:166-182.

SAS Institute. 1990. SAS/STAT user's guide. Version 6, 4th ed. SAS Institute, Cary, NC.

Swennen, C., J. C. H. Ursem, and P. Duiven. 1993. Determinate laying and egg attendance in Common Eiders. Ornis Scandica 24:48-52.

Thompson, S. C., and D. G. Raveling. 1987. Incubation behavior of Emperor Geese compared with other geese: interactions with predation, body size, and energetics. Auk 104:707-716.

Weller, M. W. 1956. A simple field candler for waterfowl eggs. Journal of Wildlife Management 20:111-113.

Zar, J. H. 1999. Biostatistical Analysis, 4th ed. Prentice Hall, New Jersey.

Zicus, M. C., S. K. Hennes, and M. R. Riggs. 1995. Common Goldeneye nest attendance patterns. Condor 97:461-472.

Table 2.1. Incubation constancy, recess length, and recess frequency for King Eiders at Teshekpuk and Kuparuk, Alaska in 2002-2005. Means, standard errors, number of females, and number of days are presented.

Site	Year	Incubation Constancy (% time on nest)	Recess Length (minutes)	Recess Frequency ($days^{-1}$)
Kuparuk	2002	99.0 ± 0.3 (8, 68)	21.46 ± 3.85 (8, 68)	0.43 ± 0.08 (8, 68)
	2003	99.0 ± 0.4 (5, 62)	22.94 ± 4.04 (5, 62)	0.58 ± 0.09 (5, 62)
	2004	99.0 ± 0.3 (7, 56)	22.40 ± 4.37 (7, 56)	0.64 ± 0.11 (7, 56)
	2005	98.0 ± 1.0 (10, 96)	23.65 ± 4.28 (10, 96)	0.708 ± 0.06 (10, 96)
Teshekpuk	2002	98.0 ± 1.0 (6, 43)	32.39 ± 5.56 (6, 43)	0.65 ± 0.13 (6, 43)
	2003	97.0 ± 1.0 (11, 112)	28.48 ± 3.46 (11, 112)	0.65 ± 0.07 (11, 112)
	2004	99.0 ± 1.0 (8, 83)	28.48 ± 5.14 (8, 83)	0.44 ± 0.10 (8, 83)
	2005	95.0 ± 3.0 (11, 127)	51.18± 14.18 (11, 127)	0.57 ± 0.08 (11, 127)

Table 2.2. General linear models of incubation constancy of female King Eiders. Calculated from females (n = 66) nesting at Teshekpuk and Kuparuk, Alaska, 2002-2005. Only the top eight models, which carry 95% of the weight, are shown. The deviance (Deviance), number of estimated parameters (K), difference in AIC_c value of each model relative to the top model (ΔAIC_c), and Akaike weights (w_i) are shown for each model. Models incorporated parameters of year, site, and island/mainland nest location.

Model	Deviance	K	ΔAIC_c[a]	w_i
Site	0.43	3	0.00	0.26
Site, year	0.39	6	0.41	0.21
Year	0.41	5	1.07	0.15
Site, year, island	0.39	7	2.11	0.09
Site, island	0.43	4	2.19	0.09
Year, island	0.40	6	2.47	0.08
Island	0.45	3	3.06	0.06
Site, island, site*island	0.43	5	4.41	0.03

[a] The lowest AIC_c value was -325.5.

Table 2.3. General linear models of daily incubation constancy of female King Eiders (n = 44) nesting at Teshekpuk and Kuparuk, Alaska. Only the top five models, which carry 95% of the weight, are shown. The deviance (Deviance), number of estimated parameters (K), difference in AIC_c value of each model relative to the top model (ΔAIC_c), and Akaike weights (w_i) are shown for each model. Models incorporated parameters of minimum daily temperature (min), maximum daily temperature (max), nest age (age), and site.

Model	Deviance	K	ΔAIC_c[a]	w_i
Min, max	4.44	4	0	0.33
Min	4.47	3	0.47	0.26
Min, max, age	4.44	5	1.96	0.12
Min, site	4.46	4	2.09	0.12
Min, age	4.46	4	2.23	0.11

[a] The lowest AIC_c value was -1786.87.

Table 2.4. Body mass of King Eider females during the breeding season. Calculated from females trapped and weighed (g ± standard error, sample size) upon arrival to the breeding grounds and at late incubation (18-23 days), at Teshekpuk and Kuparuk, Alaska, 2002-2005. Individuals were captured once within a season.

	Kuparuk		Teshekpuk	
Year	Pre-breeding	Late-incubation	Pre-breeding	Late-incubation
2002	1616 ± 92 (9)	1191 ± 22 (7)	-	-
2003	1760 ± 78 (3)	1173 ± 39 (12)	-	1113 ± 62 (6)
2004	1753 ± 53 (8)	-	1541 ± 132 (5)	-
2005	1723 ± 117 (4)	1183 ± 24 (13)	1805 ± 3 (3)	1174 ± 56 (7)

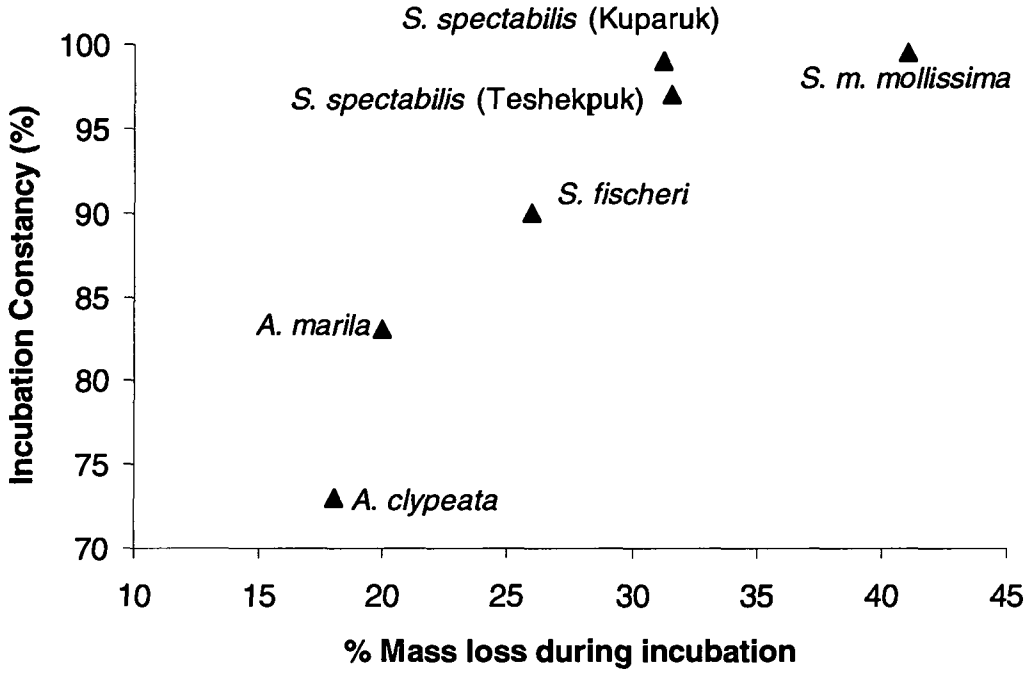

Figure 2.1. The relationship between incubation constancy and average mass loss during incubation. Included are three eider and two other waterfowl species that nest in the subarctic, *A. clyptea* and *A. marila*. Source of incubation data: *A. clyptea*, MacCluskie and Sedinger (1999) and Afton and Paulus (1992); *A. marila*, Flint (2003); *S. fischeri*, Flint and Grand (1999); *S. spectabilis*, this study; *S. m. mollissima*, Bolduc and Guillemette (2003).

3. CHARACTERIZING THE NUTRITIONAL STRATEGY OF INCUBATING KING EIDERS *SOMATERIA SPECTABILIS* IN NORTHERN ALASKA[1]

3.1. Abstract

We measured plasma concentrations of variables associated with lipid metabolism (free fatty acids, glycerol, triglyceride, and β-hydroxybutyrate), protein metabolism (uric acid), and baseline corticosterone to characterize the nutritional state of incubating King Eiders *Somateria spectabilis* and relate this to incubation constancy at two sites (Kuparuk and Teshekpuk) in northern Alaska. King Eiders at both sites appeared to employ a partial-income incubation strategy, relying on both endogenous and exogenous energy resources. Females maintained high invariant levels of free fatty acids, β-hydroxybutyrate, and glycerol throughout incubation, indicating that fat reserves were a major energy source, and not completely depleted during incubation. Similarly, uric acid did not increase, suggesting effective protein sparing or protein ingestion and adequate lipid reserves throughout incubation. Baseline corticosterone and triglyceride levels increased during incubation, indicative of an increase in foraging during late stages of incubation. Incubating females at Kuparuk had higher triglyceride concentrations but also had higher β-hydroxybutyrate concentrations than females at Teshekpuk. This dichotomy may reflect a short-term signal of feeding overlaying the longer-term signal of reliance on

[1] Bentzen, R. L., A. N. Powell, T. D. Williams, and A. S. Kitaysky. 2008. Characterizing the nutritional strategy of incubating king eiders Somateria spectabilis in northern Alaska. Journal of Avian Biology 39: 683-690.

endogenous lipid reserves due to higher food intake yet higher metabolic costs at Kuparuk because of its colder environment. Incubation constancy was not correlated with plasma concentrations of lipid or protein metabolites.

3.2. Introduction

Female waterfowl rely to a varying degree on stored reserves to meet their maintenance needs during incubation, ranging from total reliance on endogenous reserves to near total reliance on exogenous resources (Afton and Paulus 1992). The importance of endogenous reserves for successful incubation has been demonstrated in several arctic-nesting waterfowl, including lesser snow geese *Chen caerulescens caerulescens* (Ankney and MacInnes 1978), and common eiders *Somateria mollissima* (Parker and Holm 1990). Afton and Paulus (1992) asserted that incubation behavior is strongly correlated with body size; larger species are able to accumulate more endogenous reserves and therefore can maintain higher incubation constancy (i.e. the percentage of time spent incubating eggs). This may also be seen at the individual level; females with greater body reserves can afford to feed less, resulting in higher incubation constancies. Females can benefit from increased incubation constancy through increased egg-hatchability (Afton and Paulus 1992), shortened incubation periods (Zicus et al. 1995), and increased egg survival as the majority of egg predation likely occurs during incubation recesses (Swennen et al. 1993). Thus, higher incubation constancy is positively related to nest success.

King Eiders *S. spectabilis* are near the extremes of the waterfowl continuum in severity of climate at the nesting grounds and reliance on nutrient reserves for reproduction (Kellett 1999), although little is known about their breeding strategies. They are close in body size, mass loss during incubation, and incubation constancy to common eiders (Parker and Holm 1990, Kellett and Alisauskas 2000, Bolduc and Guillemette 2003), which arrive on the breeding grounds with large endogenous stores and fast throughout egg laying and incubation (Bolduc and Guillemette 2003). King Eiders have been classified as relying primarily on endogenous reserves during incubation (Lawson 2006). However, we have observed feeding during incubation, but the degree to which they rely on exogenous resources is unknown. Feeding during incubation is likely a mechanism to slow the rate of mass loss, not prevent it entirely, and may allow females to complete incubation within a safe margin of body mass (Mallory and Weatherhead 1993, Criscuolo et al. 2002). Waterfowl breeding strategies vary with the individual, and additionally appear to be spatially and temporally flexible at the population level (Klaassen et al. 2006). King Eiders may differ in nutritional strategies between population segments for example, incubation constancy varies between sites in northern Alaska while mass loss does not (R. L. Bentzen, unpubl. data). This suggests that food intake rates are variable between sites and that King Eiders utilize a mixed strategy of income and capital incubation.

Several studies have suggested that measurement of plasma metabolite concentrations (including triglycerides, glycerol, free fatty acids, β-hydroxybutyrate, and uric acid) provide useful information on physiological state (e.g. feeding vs. fasting;

Williams et al. 1999, Jenni and Schwilch 2001) and patterns of fuel utilization (Jenni-Eiermann et al. 2002), and that baseline corticosterone (CORT) can be a reliable hormonal indicator of nutritional condition in various avian species (Love et al. 2005). Plasma triglycerides are the main form in which lipids are transported to the adipose tissues. Mobilization of triglycerides releases glycerol and free (non-esterified) fatty acids. Free fatty acid concentrations are usually regarded as proportional to fatty-acid release and oxidation, and plasma glycerol levels to glycerol turnover (see Jenni-Eiermann and Jenni 1996). β-hydroxybutyrate is primarily synthesized during fasting, replacing part of the demand for glucose, especially in the brain (Robinson and Williamson 1980) and is an indicator of lipid catabolism, glucose shortage and fasting (Jenni-Eirmann and Jenni 1996). Uric acid is the main end product of nitrogen excretion in birds and as such can be used as an index of protein catabolism (Boismenu et al. 1992). CORT is known to play a key role in promoting gluconeogenesis, especially from protein (Chester-Jones et al. 1972), and is an important mediator regulating the use of endogenous energy stores (Robin et al 1988, Groscolas and Robin 2001) and stimulating foraging (Astheimer et al. 1992). As incubation progresses, females may rely on exogenous resources, endogenous stores (lipid and protein), or a combination of the two. Females relying on endogenous stores may begin mobilizing protein stores when lipid reserves are depleted.

We evaluated the nutritional condition of incubating female King Eiders by measuring levels of circulating corticosterone, and lipid and protein metabolites across incubation at two sites (Kuparuk and Teshekpuk) on the coastal plain of northern Alaska.

Additionally we investigated the relationship between the nutritional state of incubating females and incubation constancy. We hypothesized that King Eiders rely primarily on fat reserves during incubation, but also feed during incubation recesses. We predicted that, as body stores are depleted during incubation; (1) CORT would increase to redirect behavioral and metabolic processes from reproduction to foraging and promote gluconeogenesis (Chester-Jones et al. 1972), (2) triglyceride, free fatty acids, and uric acid levels would remain constant, reflecting constant lipid transport to the tissues, protein intake, and adequate fat reserves, and (3) glycerol and β-hydroxybutyrate would increase as lipids are mobilized from the tissues (Jenni-Eiermann and Jenni 1996, Hollmén et al. 2000).

Second, we hypothesized that females nesting at Kuparuk must have similar food intake rates to those females nesting at Teshekpuk in order to maintain similar mass loss rates, despite higher incubation constancy rates. We predicted that plasma metabolite levels would not differ between sites. Third, we hypothesized that at the individual level and assuming that food availability remains the same, as incubation constancy decreases, food intake rates would increase and lipid mobilization would decrease, due to a trade-off between incubation constancy and time spent foraging for exogenous resources. We predicted that as incubation constancy decreases, triglyceride and uric acid levels would increase, and that glycerol, free fatty acids and β-hydroxybutyrate levels would decrease.

3.3. Methods

3.3.1. Study area and nest searches

We studied King Eiders nesting at two sites on the North Slope of Alaska, one near Teshekpuk Lake (153° 07'W, 70° 25'N) and another within the Kuparuk oilfields (149° 41'W, 70° 27'N) in 2005 and 2006. The Teshekpuk study site was approximately 10 km inland from the southeast shore of Teshekpuk Lake and has experienced minimal human impact. The Kuparuk study site was in an area between the Colville and Kuparuk river deltas developed for oil production. Temperatures at Kuparuk were cooler during the years of the study (minimum daily temperature averaged 1.5° C lower; R. L. Bentzen, unpubl. data). We systematically searched wetland basins on foot for King Eider nests, beginning in mid-June at both sites. We calculated nest-initiation dates from estimated incubation stages as determined by candling eggs (Weller 1956), assuming a laying interval of one egg per day and an incubation length of 23 d (Lamothe 1973).

3.3.2. Field methods

We opportunistically placed data loggers (HOBO-TEMP, Onset Computer Corporation) in nests at Teshekpuk and Kuparuk, and programmed them to record nest temperature every 2 min (n = 14) in 2005. We used blown chicken eggs, dyed an olive green and attached to a bolt, to hold the thermistor probes. The bolt was driven into the ground under the nest, anchoring the probe and dummy egg in the nest (see Quakenbush et al. 2004). This allowed for a quick response to any change in temperature because the probe had only an eggshell between it and the incubating female. We defined incubation

constancy as the percentage of time the female was on her nest over the week prior to blood sampling.

We trapped female King Eiders on the nest using a drop or bow net between mid-incubation (8 d after initiation of incubation), and hatch (23 d after initiation) at both sites in 2005 and at Kuparuk in 2006. Blood samples (~500 μl) were collected via jugular venipuncture and transferred to microcentrifuge tubes; syringes and microcentrifuge tubes were treated with heparin prior to use. We kept blood samples on ice and centrifuged within 3 h of collection to separate plasma from red blood cells, and froze plasma immediately after separation. We took samples within 3 min of capture to determine baseline CORT and corticosterone-binding globulin (CBG) levels at Kuparuk in 2005 ($n_{Kuparuk} = 20$) and 2006 ($n_{Kuparuk} = 7$), and within 10 min of capture to determine fat metabolite levels in 2005 at both sites ($n_{Kuparuk} = 22$; $n_{Teshekpuk} = 13$). Blood samples were collected once per bird; if blood sampling took longer than 3 min, we did not assay for CORT. We captured four individuals at Kuparuk in both mid and late incubation in 2005; all other individuals were captured only once in a season. We banded (USFWS aluminum bands) and weighed all captured birds.

3.3.3. Metabolite determinations

We assayed plasma samples for five metabolites: free glycerol, triglyceride, β-hydroxybutyrate, free fatty acids, and uric acid (following Guglielmo et al. 2002 and Seaman et al. 2005). Metabolite concentrations were determined at Simon Fraser University using a Powerwave 340× microplate spectrophotometer (BioTec Instruments,

USA). We ran assays in 400 µl flat-bottom, 96-well polystyrene microtitre plates (NUNC, Denmark), and measured free glycerol and triglycerides sequentially by endpoint assay (Sigma; 5 µl plasma, 240 µl reagent A, 60 µl reagent B); free fatty acids were measured by endpoint assay (WAKO Diagnostics, Richmond, VA; 5 µl sample, 100 µl reagent A, 200 µl reagent B, read at 550 nm). We measured uric acid using a Quantichrom endpoint assay kit (BioAssay Systems, Hayward, CA; 5 µl sample, 200 µl working reagent, read at 590 nm) and β-hydroxybutyrate by kinetic assay (Megazyme; D3-HBA reagent; 10 µl sample, 272 µl working reagent, 2 µl enzyme, read at 492 nm). Intra-assay coefficients of variation (CV%) were 3.6% (n = 10) for glycerol, 3.3% (n = 10) for triglyceride, 4.0% (n = 12) for β-hydroxybutyrate, 4.2% (n = 15) for free fatty acids, and 5.7% (n = 9) for uric acid. Inter-assay CV% was 6.0% and 5.6% respectively (n = 17; eider samples were assayed with other samples). All samples for β-hydroxybutyrate, free fatty acids, and uric acid were assayed in only two plates per metabolite and mean metabolite concentrations for a Sigma hen pool were 2.21 and 2.09 mmol/l, 0.616 and 0.599 µmol/l, and 0.550 and 0.548 mmol/l, respectively, for the two plates.

3.3.4. Corticosterone determinations

We determined total plasma levels of CORT with a radioimmunoassay (Wingfield et al. 1992) at the University of Alaska, Fairbanks. CORT concentrations were measured in duplicate for each plasma sample after extraction in dichloromethane. We used recovery values (87 - 99%) following extractions to adjust assayed concentrations of CORT. We processed all samples collected in 2005 in one assay and samples collected in 2006 in a second assay. Intra- and inter-assay CV% were < 2%.

We used radioligand binding methods for measuring corticosterone binding globulin (CBG) based on those described in Deviche et al. (2001). We optimized incubation time (2 h), plasma dilution (1:198), and tritiated CORT concentration (6nM ^{3}H) for King Eiders. Affinity (Kd) estimates were 9.2nM. The intra-assay CV% was 1%. We estimated free CORT concentrations using the equation of Barsano and Baumann (1989), outlined in Deviche et al. (2001).

3.3.5. Statistical analysis

We examined variation in body mass in relation to day of incubation using analysis of covariance (ANCOVA) with site as a factor and day of incubation as a covariate (SAS Institute 1990). To investigate patterns of fuel utilization across incubation and between sites, we examined relationships among plasma chemistry variables and age of the nest (day of incubation) at Kuparuk and Teshekpuk using ANCOVA. Additionally, we examined variation in plasma levels of baseline total and free CORT and CBG binding capacity between years (2005-2006) and age of the nest using ANCOVA. We adjusted P-values using the Benjamini-Hochberg false discovery rate (Benjamini and Hochberg 1995). We examined residuals for normality (Shapiro-Wilk, $P > 0.05$), outliers and influential observations, and homoscedasticity. Uric acid and free CORT concentrations were log transformed to meet the assumptions of ANCOVA. We included first order interactions between factors and covariates and removed nonsignificant interactions from the final models based on type III mean square errors.

We used the nonparametric Mardia-Watson-Wheeler test for more than two samples (Zar 1999) to determine if the distribution of timing of trapping females differed between sites. This analysis was conducted using Oriana (Kovach Computing Services 2005). Given the non-von Mises distribution of trap times (Watson's U^2-test, $U^2 = 0.12$, $P = 0.03$), and low concentrations, we used a linear nonparametric approach to correlate timing of trapping with metabolite level (Spearman's R) and examined the graphs for nonlinear relationships. We adjusted P-values from the five correlations using the Benjamini-Hochberg false discovery rate (Benjamini and Hochberg 1995).

Lastly, we investigated the hypothesis that, at the individual level, as incubation constancy decreases, food intake rates increase and lipid mobilization decreases. We used general linear models (PROC GLM; SAS Institute 1990) to evaluate the relationship between plasma concentrations of triglyceride, free fatty acid, uric acid, body mass and site on incubation constancy the week prior to blood sampling, while controlling for age at capture, using 6 *a priori* candidate models (n = 14). We did not include CORT in the models as it severely limited the dataset. We excluded plasma concentrations of β-hydroxybutyrate and glycerol from the model set to reduce the number of models investigated. We did not include any nonlinear or interaction terms due to the limited dataset. Constancy was transformed to the arcsine of the square root to improve normality (Shapiro-Wilk, $P > 0.05$). We used Akaike's information criterion adjusted for small sample size (AIC_c) to select the best approximating models as it allowed us to evaluate a number of competing nested models without violating the rules of multiple comparisons

and error rates (Burnham and Anderson 2002). Values are reported as means ± SE (or circular SD).

3.4. Results

We captured a total of 48 female eiders during days 8-23 of incubation at Teshekpuk and Kuparuk, Alaska, 2005 and 2006; however levels of corticosterone, triglyceride, glycerol, β-hyrdoxybutyrate, free fatty acids and uric acid were not all measured in all females. During this period of incubation females lost an average of 18.4 (± 3.6; $F_{1,45} = 26.31$, $P < 0.05$) g day^{-1}, and weight loss was not different between sites ($F_{1,45} = 0.65$, $P > 0.05$). The four females trapped during both mid- and late-incubation lost an average of 19.1 (± 3.0) g day^{-1}. On average females weighed 1214.6 (± 21.9) g at the end of incubation (>18 days incubation).

Triglyceride levels increased with nest age ($F_{1,33} = 4.84$, $P < 0.05$) while β-hydroxybutyrate ($F_{1,29} = 0.61$, $P > 0.05$), glycerol ($F_{1,33} = 0.81$, $P > 0.05$), free fatty acids ($F_{1,31} = 0.06$, $P > 0.05$), and uric acid did not vary with nest age ($F_{1,30} = 3.59$, $P > 0.05$; Fig. 3.1). Triglyceride levels were higher at Kuparuk (0.86 ± 0.07 mmol/l, n = 23) than Teshekpuk (0.52 ± 0.09 mmol/l, n = 13; $F_{1,33} = 9.19$, $P < 0.05$), as was β-hydroxybutyrate (Kuparuk 3.08 ± 0.22 mmol/l, n = 22, Teshekpuk 2.05 ± 0.31 mmol/l, n = 10; $F_{1,29} = 6.76$, $P < 0.05$). Glycerol was lower at Kuparuk than Teshekpuk (Kuparuk 0.28 ± 0.02 mmol/l, n = 23, Teshekpuk 0.39 ± 0.05 mmol/l, n = 13; $F_{1,33} = 5.45$, $P < 0.05$), while free fatty acids (0.66 ± 0.06 mmol/l, n = 34) and uric acid (0.27 ± 0.03 mmol/l, n = 33) did not vary between sites (FFA, $F_{1,31} = 0.41$, $P > 0.05$; uric $F_{1,30} = 1.61$, $P > 0.05$). Females

were trapped between 09.26 and 21.50 h at Kuparuk and 09.27 and 19.33 at Teshekpuk and the distribution of trap times varied between Kuparuk (14.29 h ± 286 min) and Teshekpuk (12.52 h ± 96 min; $W = 7.06$, P = 0.03). However, plasma levels of the five metabolites were not significantly correlated with trap time (Spearman's $R < |0.03|$, P > 0.05).

Further analysis indicated that total and free CORT increased with nest age ($F_{total, 1,23} = 7.58$, P < 0.05; $F_{free, 1,23} = 11.83$, P < 0.05; Fig. 3.2) while CBG binding capacity did not vary with nest age ($F_{1,23} = 1.56$, P > 0.05). Free CORT and CBG binding capacity did not vary between years ($F_{1,23} < 2.3$, P > 0.05), while total CORT was higher in 2006 than 2005 ($F_{1,23} = 5.32$, P < 0.05). Total CORT was not correlated with any of the metabolites in 2005 ($R < 0.34$, n = 18, P > 0.05). Plasma metabolite levels were not determined in 2006.

King Eiders had very high incubation constancy (0.98 ± 0.01, % time on nest). Females took an average of 0.61 (± 0.08) recesses day^{-1}, with an average length of 31(± 8) min. We did not find any correlation between incubation constancy the week prior to blood sampling and plasma concentrations of triglycerides ($\beta_{triglyceride}$ = -0.004, 95% CI = -0.1.06, 0.099), uric acid (β_{uric}= -0.210, 95% CI = -0.605, 0.185), or free fatty acids (β_{FFA} = > 0.000, 95% CI = -0.104, 0.105; Table 3.1). The top model was 8.5 AIC_c units from the next best model and supported an effect of body mass and nest age at capture on incubation constancy. Incubation constancy the week prior to trapping increased with

body mass (β_{mass} = 0.001, 95% CI = 0.000, 0.001) and nest age (β_{age} = 0.009, 95% CI = 0.002, 0.017), although the size of the effect was small.

3.5. Discussion

Our data suggest that King Eider females nesting on Alaska's North Slope relied on both endogenous and exogenous energy resources during incubation, as hypothesized. However, levels of plasma metabolites across incubation differed from our predictions in some cases. Constant levels of free fatty acids, β-hydroxybutyrate, and glycerol were maintained throughout incubation indicating that fat reserves were not, in general, completely depleted during incubation (Le Maho et al. 1981, Groscolas 1986, Hollmén et al. 2000). Contrary to our predictions, plasma triglycerides actually increased over incubation, suggesting that King Eiders were feeding throughout incubation and that total food intake increased as incubation progressed. Plasma uric acid concentrations did not increase in King Eiders during incubation, indicating either effective protein sparing and adequate lipid reserves remaining through the end of incubation, or feeding rates high enough to prevent endogenous protein utilization and providing a constant intake of exogenous protein.

In fasting birds uncontrolled elevation of CORT concentration may lead to protein catabolism and therefore to the disturbance of lipid use and of the overall energetic balance (Cherel et al. 1988). Accordingly, common eiders (a capital breeder) maintain low thresholds of CORT throughout incubation; at least until body lipids are depleted, potentially to reduce body protein mobilization for energy supply (Criscuolo et al. 2006).

However, in an income-breeder that feeds to some extent during incubation, CORT may increase as body reserves are depleted redirecting behavioral and metabolic processes from reproduction to foraging (Astheimer et al. 1992). King Eiders showed both an increase in CORT and lipid transport to the tissues over the incubation period, indicating that they utilized a partial-income incubation strategy. It is likely that increased CORT stimulated foraging, thus increasing triglyceride levels and preventing depletion of the fat reserve (i.e. maintaining constant levels of lipid transport from the tissues). Potentially the increase in CORT allowed effective fat and protein sparing and thus the constant levels of β-hydroxybutyrate, glycerol, and free fatty acids across incubation; however, we found no correlation between CORT and triglyceride levels. This may be due to the small sample size of females where both CORT and triglyceride levels were measured. Interestingly, we detected an increase in both free and total CORT during incubation. There appeared to be no buffering of the 'active' portion of the hormone titer by CBGs, indicating that the increase of total CORT was biologically relevant.

A partial-income strategy does not necessarily imply primary reliance on exogenous resources. King Eiders loose ~ 30% of their pre-incubation body mass during incubation (this study, Kellett and Alisauskas 2000) and are certainly relying heavily on lipid reserves. Published concentrations of glycerol (mean ± SD; 288 ± 124 μmol/l),β-hydroxybutyrate (3.20 ± 1.92 mmol/l), and triglyceride (1.02 ± 0.37mmol/l) in common eiders (Hollmén et al. 2000) during late incubation were very similar to those found in King Eiders, suggesting they have similar incubation strategies, both relying primarily on endogenous reserves. However, Hollmén et al. (2000) showed that, in some years,

common eiders might transition to utilization of body proteins as a primary energy source after depleting their lipid reserves. We found no evidence of this in King Eiders, however, we only examined one year and patterns of resource utilization may vary among years. King Eiders may be able to prevent the depletion of lipid reserves through foraging throughout incubation and thus may not need to transition to body protein use in late incubation.

We predicted that eiders nesting at Kuparuk, which exhibited higher incubation constancy yet maintained similar weight loss to those at Teshekpuk, would show similar lipid transport to the tissues, indicating similar food intake rates, and similar rates of lipid mobilization from the tissues, reflecting similar mass loss. However, our results were more complex; higher triglyceride concentrations at Kuparuk indicated that females fed more relative to Teshekpuk (see Jenni-Eiermann and Jenni 1996), but higher β-hydroxybutyrate at Kuparuk indicated a higher rate of lipid mobilization in birds there (Le Maho et al. 1981, Groscolas 1986). This pattern may be reflective of short-term feeding during incubation breaks generating a transient "feeding" signal in terms of elevated triglyceride which overlays the longer-term "fasting" signal of elevated β-hydroxybutyrate over the course of incubation with different rates of metabolic response to feeding among the metabolites. There is some evidence for different rates of metabolic responses to feeding, but only over a short time scale and in passerines (Jenni-Eiermann and Jenni 1996, Zajac et al. 2006). The disjunct in King Eiders on the coastal plain of Alaska could reflect differences in site quality or ambient temperature. Temperatures at Kuparuk were cooler during the years of our study, which potentially lead to a greater

cost of incubation (Fast et al. 2007). In addition, if females must expend more energy incubating, but also have access to higher quality food, we could see this pattern of higher food intake and higher levels of lipid mobilization. It would be expected that CORT levels would also vary between sites given the difference in triglyceride levels, however, we were unfortunately unable to pursue this due to sample size limitations.

Incubating King Eider females generally take one break per day, in the afternoon, (R. L. Bentzen, unpubl. data) and have been observed feeding during these times. Since triglyceride and β-hydroxybutyrate levels can respond within 10-20 min to an increase in feeding rate (Zajac et al. 2006), timing of trapping in relation to daily feeding bouts could affect the results and could potentially explain the observed site differences. However, we do not feel that this can explain the observed site differences, as there were no correlations between trap time and metabolite level.

In conclusion, King Eider females nesting on Alaska's North Slope relied on both endogenous and exogenous energy resources during incubation. Fat reserves were not, in general, completely depleted during incubation, potentially because females were feeding and total food intake increased as incubation progressed. Increased CORT across incubation may have stimulated this foraging, increasing triglyceride levels and preventing fat reserve depletion (i.e. maintaining constant levels of lipid transport from the tissues) and may have allowed effective fat and protein sparing. Females at Kuparuk had higher food intake rates relative to Teshekpuk but also higher rates of lipid mobilization. This dichotomy may reflect a short-term signal of feeding overlaying the

longer-term signal of reliance on endogenous lipid reserves. It may indicate that females expended more energy incubating (cooler ambient temperatures), but also had access to higher quality food at Kuparuk. Food resources on the breeding grounds evidently play an important role in King Eider reproduction.

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3.7. Literature cited

Afton, A. D. and Paulus, S. L. 1992. Incubation and brood care. – In: Batt, B. D. Afton, A. D., Anderson, M. G., Ankney, C. D., Johnson, D. H., Kadlec, J. A. and Krapu, G. L. (eds). Ecology and management of breeding waterfowl. University Minnesota Press, Minneapolis, pp. 62-108.

Ankney, C. D. and MacInnes, C. D. 1978. Nutrient reserves and reproductive performance of female lesser snow geese. – Auk 95: 459-471.

Astheimer, L. B., Buttemer, W. A. and Wingfield, J. C. 1992. Interactions of corticosterone with feeding, activity and metabolism in passerine birds. – Ornis Scand. 23: 355-365.

Barsano, C. P. and Baumann, G. 1989. Editorial; simple algebraic and graphic methods for the apportionment of hormone (and receptor) into bound and free fractions in binding equilibria; or how to calculate bound and free hormone? – Endocrin. 124: 1101-1106.

Benjamini, Y. and Hochberg, Y. 1995. Controlling the false discovery rate: a practical and powerful approach to multiple testing. – J. R. Stat. Soc. B 57: 289-300.

Boismenu, C., Gauthier, G. and Larochelle, J. 1992. Physiology of prolonged fasting in greater snow geese (*Chen caerulensis atlantica*). – Auk 109: 511-521.

Bolduc, F. and Guillemette, M. 2003. Incubation constancy and mass loss in the common eider *Somateria mollissima*. – Ibis 145: 329-332.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. – Springer-Verlag, New York.

Cherel, Y., Robin, J. -P. and Le Maho, Y. 1988. Physiology and biochemistry of long-term fasting in birds. – Can. J. Zool. 66: 159-166.

Chester-Jones, I., Bellamy, D., Chan, D. K. O., Follett, B. K., Henderson, I. W., Phillips, J. G. and Snart, R. S. 1972. Biological actions of steroid hormones in non-mammalian vertebrates. – In Idler, D. R. (ed.). Steroid in non-mammalian vertebrates. Academic Press, New York, pp. 414-480.

Criscuolo, F., Gabrielsen, G. W., Gendner, J. –P. and Le Maho, Y. 2002. Body mass regulation during incubation in female common eiders *Somateria mollissima*. – J. Avian Biol. 33: 83-88.

Criscuolo, F., Bertile, F., Durant, J. M., Raclot, T., Gabrielsen, G. W., Massemin, S. and Chastel, O. 2006. Body mass and clutch size may modulate prolactin and corticosterone levels in eiders. – Physiol. Biochem. Zool. 79: 514-521.

Deviche, P., Breuner, C. W. and Orchinik, M. 2001. Testosterone, corticosterone, and photoperiod interact to regulate plasma levels of binding globulin and free steroid hormone in dark-eyed juncos, *Junco hyemalis*. – Gen. Comp. Endocrinol. 122: 67-77.

Fast, P. L. F., Gilchrist, H. G. and Clark, R. G. 2007. Experimental evaluation of nest shelter effects on weight loss in incubating common eiders *Somateria mollissima*. – J. Avian Biol. 38: 205-213.

Groscolas, R. 1986. Changes in body mass, body temperature and plasma fuel levels during the natural breeding fast in male and female emperor penguins *Aptenodytes forsteri*. – J. Comp. Physiol. B. 156: 521-527.

Groscolas, R. and Robin, J.-P. 2001. Long-term fasting and re-feeding in penguins. – Comp. Biochem. Physiol. A 128: 645-655.

Guglielmo, C. G., O'Hara, P. D. and Williams, T. D. 2002. Extrinsic and intrinsic sources of variation in plasma lipid metabolites of free-living western sandpipers (*Calidris mauri*). – Auk 119: 437-445.

Hollmén, T., Franson, J. C., Hario, M., Sankari, S., Kilpi, M. and Lindström, K. 2000. Use of serum biochemistry to evaluate nutritional status and health of incubating common eiders (*Somateria mollissima*) in Finland. – Physiol. Biochem. Zool. 74: 333-342.

Jenni, L. and Schwilch, R. 2001. Plasma metabolite levels indicate change in body mass in reed warblers *Acrocephalus scirpaceus*. – Avian Science 1: 55-65.

Jenni-Eiermann, S. and Jenni, L. 1996. Metabolic differences between the postbreeding, moulting and migratory periods in feeding and fasting passerine birds. – Funct. Ecol. 10: 62-72.

Jenni-Eiermann, S., Jenni, L. and Piersma, T. 2002. Plasma metabolites reflect seasonally changing metabolic processes in a long-distance migrant shorebird (*Calidris canutus*). – Zoology 105: 239-246.

Kellett, D. K. 1999. Causes and consequences of variation in nest success of king eiders (*Somateria spectabilis*) at Karrak Lake, Northwest Territories. – M.Sc.Thesis, University of Saskatchewan, Saskatoon.

Kellett, D. K. and Alisauskas, R. T. 2000. Body-mass dynamics of king eiders during incubation. – Auk 117: 812-817.

Klaassen, M., Abraham, K. F., Jefferies, R. L. and Vrtiska, M. 2006. Factors affecting the site of investment, and the reliance on savings for arctic breeders: the capital-income dichotomy revisited. – Ardea 94: 371-384.

Kovach Computing Services. 2005. Oriana version 1. – Kovach Computing Services, Anglesey, Wales.

Lamothe, P. 1973. Biology of the king eider (*Somateria spectabilis*) in a freshwater breeding area on Bathurst Island, N.W.T. – M.Sc. Thesis, University of Alberta, Edmonton, Alberta.

Lawson, S. 2006. Comparative reproductive strategies between long-tailed ducks and king eiders at Karrak Lake, Nunavut: use of energy resources during the nesting season. – M.Sc. Thesis, University of Saskatchewan, Saskatoon.

Le Maho, Y., Vu Van Kha, H., Koubi, H., Dewasmes, G., Girard, J., Ferre, P. and Cagnard, M. 1981. Body composition, energy expenditure, and plasma metabolites in long-term fasting geese. – Am. J. Physiol. 241: E342-E354.

Love, O. P., Chin, E. H., Wynne-Edwards, K. E. and Williams, T. D. 2005. Stress hormones: a link between maternal condition and sex-biased reproductive investment. – Am. Nat. 166: 751-766.

Mallory, M. L. and Weatherhead, P. J. 1993. Incubation rhythms and mass loss of common goldeneyes. – Condor 95: 849-859.

Parker, H. and Holm, H. 1990. Patterns of nutrient and energy expenditure in female common eider nesting in the high arctic. – Auk 107:660-665.

Quakenbush, L., Suydam, R., Obritschkewitsch, T. and Deering, M. 2004. Breeding biology of Steller's eiders (*Polysticta stelleri*) near Barrow, Alaska, 1991-99. – Arctic 57: 166-182.

Robin, J., Frain, M., Sardet, C., Groscolas, R. and Le Maho, Y. 1988. Protein and lipid utilization during long-term fasting in emperor penguins. – Am. J. Physiol. 254: R61-R68.

Robinson, A. M. and Williamson, D. H. 1980. Physiological roles of ketone bodies as substrates and signals in mammalian tissues. – Physiol. Review. 60: 143-187.

SAS Institute. 1990. SAS/STAT user's guide. Version 6, 4th ed. - SAS Institute, Cary.

Seaman, D. A., Guglielmo, C. G. and Williams, T. D. 2005. Effects of physiological state, mass change, and diet on plasma metabolite profiles in the western sandpiper (*Calidris mauri*). – J. Exp. Biol. 208: 761-769.

Swennen, C., Ursem, J. C. H. and Duiven, P. 1993. Determinate laying and egg attendance in common eiders. – Ornis Scand. 24: 48-52.

Weller, M. W. 1956. A simple field candler for waterfowl eggs. – J. Wild. Manage. 20: 111-113.

Williams, T. D., Guglielmo, C. G., Egeler, O. and Martyniuk, C. J. 1999. Plasma lipid metabolites provide information on mass change over several days in captive western sandpipers. – Auk 116: 994-1000.

Wingfield, J. C., Vleck, C. M. and Moore, M. C. 1992. Seasonal changes in the adrenocortical response to stress in birds of the Sonoran desert. – J. Exp. Zool. 264: 419-428.

Zajac, R. M., Cerasale, D. J. and Guglielmo C. G. 2006. The rapid response of plasma metabolites to changes in feeding rate in a small passerine Wilson's warbler *Wilsonia pusilla*. – J. Avian Biol. 37: 405-408.

Zar, J. H. 1999. Biostatistical analysis, 4th ed. – Prentice Hall, New Jersey.

Zicus, M. C., Hennes, S. K. and Riggs, M. R. 1995. Common goldeneye nest attendance patterns. – Condor 97: 461-472.

Table 3.1. Relationship between incubation constancy and metabolite levels in incubating King Eiders. General linear models of incubation constancy the week prior to blood sampling for females (n = 14) nesting at Teshekpuk and Kuparuk, Alaska, 2005. Models are sorted by AIC_c and incorporated parameters of site, nest age at trapping (age), body mass at trapping, and plasma concentrations of triglyceride, glycerol, free fatty acids, β-hydroxybutyrate, and uric acid.

Incubation constancy model	K[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	R^2
Age, mass	4	-74.33	0.00	0.98	0.60
Age	3	-65.82	8.51	0.01	0.01
Age, uric acid	4	-63.09	11.24	0.00	0.10
Age, site	4	-61.79	12.55	0.00	0.02
Age, triglyceride	4	-61.78	12.55	0.00	0.02
Age, free fatty acid	4	-61.77	12.56	0.00	0.01

[a] Number of parameters in the model.

[b] Akaike information criterion adjusted for small sample size.

[c] Difference between model AIC_c and AIC_c value of the best model.

[d] AIC_c weights.

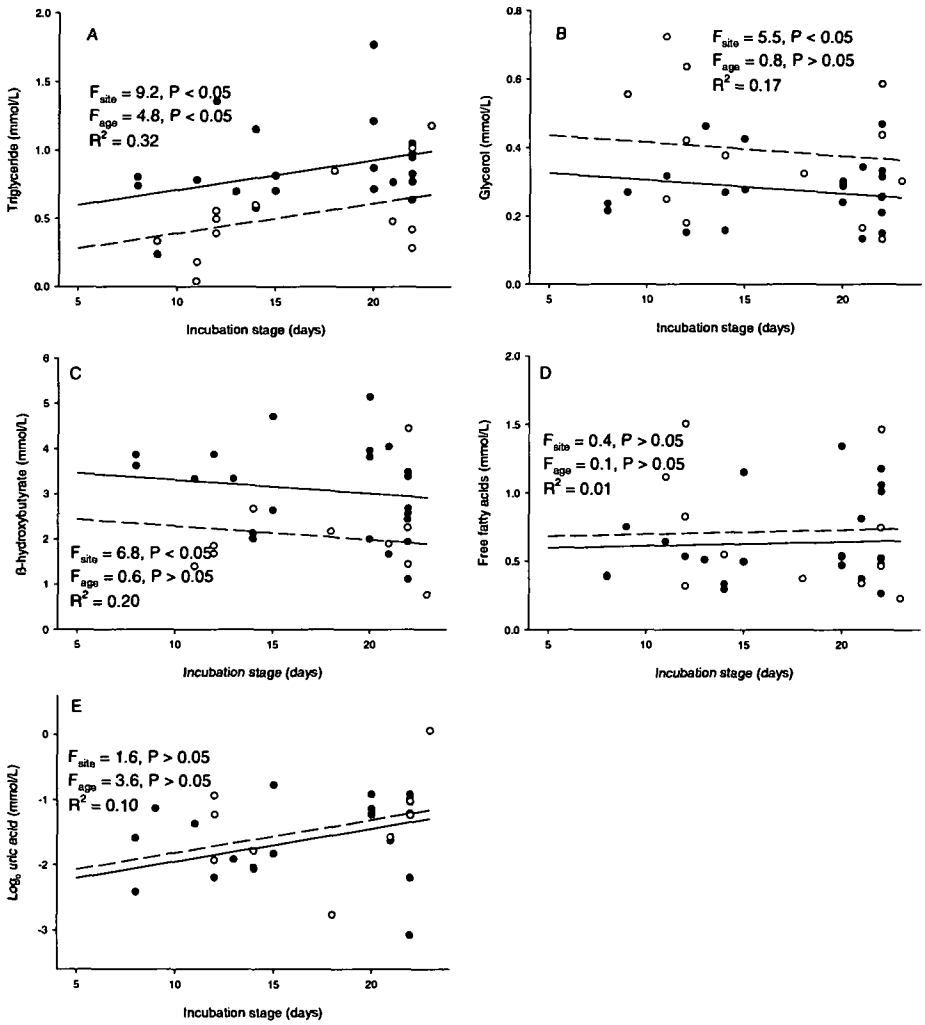

Figure 3.1. Relationship between incubation stage and metabolite level. Plasma concentrations of triglyceride (A), glycerol (B), β-hydroxybutyrate (C), free fatty acids (D) and uric acid (E), and model predictions from analysis of covariance (ANCOVA; all interactions insignificant) relating incubation stage (age) to metabolite level (with site as a factor) in King Eider *Somateria spectabilis* females at Kuparuk (filled circles, solid line) and Teshekpuk (open circles, dashed line), Alaska, 2005.

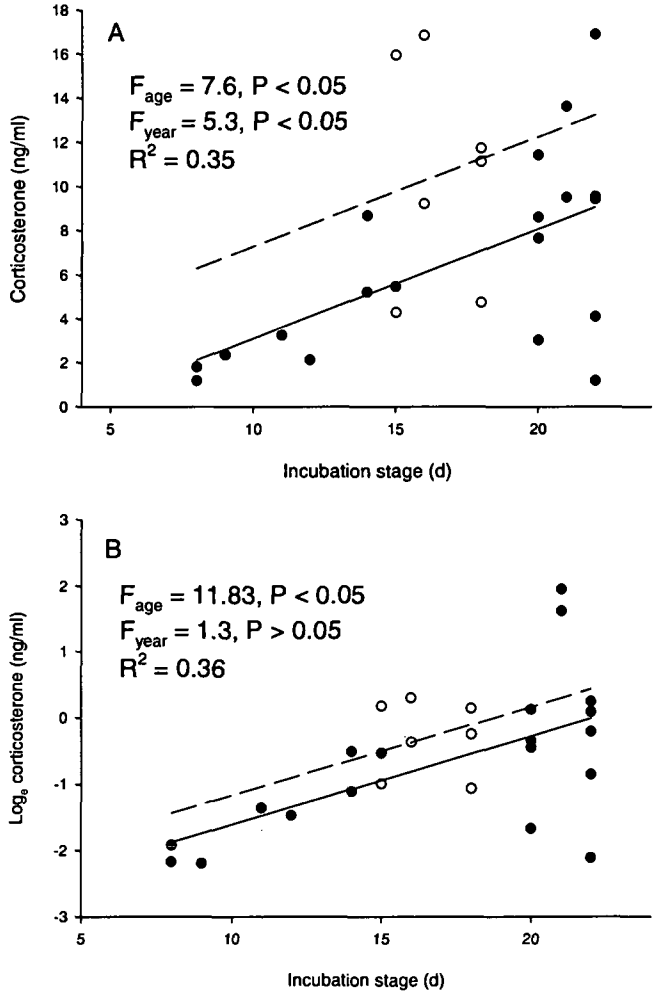

Figure 3.2. Relationship between incubation stage and corticosterone levels. Baseline total (A) and free (B) plasma levels of corticosterone during incubation and model predictions from analysis of covariance (ANCOVA; all interactions insignificant) relating incubation stage (age) to corticosterone level (with year as a factor) in King Eider *Somateria spectabilis* females at Kuparuk, Alaska, 2005 (filled circles, solid line) and 2006 (open circles, dashed line).

4. FACTORS INFLUENCING NESTING SUCCESS OF KING EIDERS ON NORTHERN ALASKA'S COASTAL PLAIN [1]

4.1. Abstract

King Eider (*Somateria spectabilis*) populations have declined markedly in recent decades for unknown reasons. Nest survival is one component of recruitment, and a female's chance of reproductive success increases with her ability to choose an appropriate nesting strategy. We estimated variation in daily nest survival of King Eiders at 2 sites, Teshekpuk and Kuparuk, Alaska, 2002-2005. We evaluated both a priori and exploratory competing models of nest survival that considered importance of nest concealment, seclusion, and incubation constancy as strategies to avoid 2 primary egg predators, avian (*Larus* spp., *Stercorarius* spp., and *Corvus Corax*) and fox (*Alopex lagopus*). We used generalized nonlinear techniques to examine factors affecting nest survival rates and information-theoretic approaches to select among competing models. Estimated nest survival, accounting for a nest visitation effect, varied considerably across sites and years (0.21- 0.57), however, given our small sample size, much of this variation may be attributable to sampling variation ($\sigma^2_{process}$= 0.007, 95% CI: 0.003–0.070). Nest survival was higher at Kuparuk than Teshekpuk in all years, however, due to the correlative nature of our data, we cannot determine the underlying causes with any certainty. We found mixed support for the concealed breeding strategy; females derived no benefit from

[1] Bentzen, R. L., A. N., Powell, and R. S. Suydam. 2008. Factors influencing nesting success of king eiders on northern Alaska's coastal plain. Journal of Wildlife Management 72: 1781-1789.

nesting in areas with more willow (*Salix* spp.; measure of concealment) except that the observer effect diminished as willow cover increased. We suggest these patterns are due to conflicting predation pressures. Nest survival was not higher on islands (measure of seclusion) or with increased incubation constancy but was higher post fox-removal, indicating that predator control on breeding grounds could be a viable management option. Nest survival was negatively affected by our nest visitations, most likely by exposing the nest to avian scavengers. We recommend precautions be taken to limit the effects of nest visits in future studies and to consider them as a possible negative bias in estimated nest survival. Future models of the impacts of development within the breeding grounds of King Eider should consider the influence of humans in the vicinity of nests.

4.2. Introduction

The western North American population of King Eiders (*Somateria spectabilis*) has declined by >50% between 1976 and 1996 for unknown reasons (Suydam et al. 2000). Eiders generally experience low and variable nest survival, one component of population recruitment (Lamothe 1973, Goudie et al. 2000, Petersen et al. 2000, Kellett et al. 2003). Reproductive success of a female depends, in part, upon successfully incubating a clutch and surviving to nest again. Any adaptations that serve to increase nest success, even slightly, may have a high selective value (Ricklefs 1984), although trade-offs between life history traits could influence selection. Although population growth rate is often considered to have a low sensitivity or elasticity with respect to nest success, high inherent variation in nesting success can influence population dynamics (Hoekman et al. 2002, Flint et al. 2006). Predators are probably the most important selective force

affecting nest success in birds (Ricklefs 1969, Martin 1995), resulting in a variety of strategies related to nest protection, including breeding synchrony, coloniality, distraction behavior, concealment, incubation behavior, and aggressive nest defense. However, options for avoiding predation are constrained by available habitat and condition of the female.

Larson (1960) argued that 2 main evolutionary strategies are used by arctic tundra-nesting birds that have a limited ability to defend their nests, secluded nesting (success is increased through greater inaccessibility of nest location) or concealed nesting (success is increased through more concealed nest location on the open tundra of the mainland and appropriate behavior). In most waterfowl, and eiders in particular, the main option for secluded breeding is to nest on islands. However, this strategy does not provide any protection from avian predators, such as gulls (*Larus* spp.) and jaegers (*Stercorarius* spp.). Concealed breeders may have some degree of protection from both avian and mammalian egg predators. The concealed breeding strategy relies on the nest and hen being camouflaged to some degree, usually by the vegetation around the nest. Hens also use behavioral strategies for concealment, including spacing of nests and choices in number and length of recesses she takes during incubation. Although King Eiders typically cover their eggs when they take a recess (Parmelee et al. 1967, Lamothe 1973), the activity of moving to and from the nest may attract predators, and while on recess the female is unable to defend the nest.

Predators of King Eider eggs fall into 2 categories, avian (gulls, jaegers, and ravens [*Corvus corax*]) and mammalian (Arctic fox [*Alopex lagopus*]; Lamothe 1973, Kellett 1999). Strategies to avoid predation likely vary between the two types of predators. Larson (1960) argued that King Eiders have an inferior to medium adaptation to fox predation, suggesting that nest site selection may have evolved in the absence of heavy fox predation. Incubating eiders are unable to defend their nests from foxes (Lamothe 1973, P. Flint, United States Geological Survey, unpublished data) and do not feign injury to draw potential predators from the nest (Larson 1960), potentially relying on strategies of seclusion (island nesting), solitary nesting, and concealment. King Eiders have been known to successfully deter predation attempts by gulls (Kellett and Alisauskas 1997) and jaegers (Blomqvist and Elander 1988) and most avian depredation events occur during periods when the incubating female is absent from the nest (P. Flint, unpublished data) and maintaining high incubation constancy is thought to be a strategy aimed at avoiding avian depredation (Milne 1976, Swennen et al. 1993, Bolduc et al. 2005). Therefore, to avoid avian predation it would be advantageous to maintain high incubation constancy and nest in an area with more cover; nests with a high degree of cover should be less obvious both when attended and unattended.

Our goal was to evaluate factors influencing nest survival of King Eiders on the coastal plain of northern Alaska. We hypothesized that King Eiders may be under competing selection pressures associated with 2 primary egg predators, avian and fox, and that nesting strategies could reflect this dual pressure. First, we predicted that nest survival would be higher on islands if King Eiders benefit from seclusion from

mammalian predators. Second, we predicted that nest survival is higher in areas with taller vegetation (concealment), as measured by percent willow near the nest, and at nests where the female maintains higher attendance rates so as to minimize avian egg depredation. We also examined other sources of variation in daily survival rates including both ecological (season date and nest age) and anthropogenic variables (observer effect) in our models.

4.3. Methods

4.3.1. Study area

We studied King Eiders nesting at 2 sites on the North Slope of Alaska, one near Teshekpuk Lake (153°07'W, 70°25'N) and another within the Kuparuk oilfields (149°41'W, 70°27'N), from 2002-2005. The Teshekpuk study site was approximately 10 km inland from the southeast shore of Teshekpuk Lake and experienced minimal human impact (i.e. no roads, communities, or development for petroleum extraction). The Kuparuk study site was in an area between the Colville and Kuparuk river deltas, which was developed for petroleum production and had an associated road network and human activities. The study sites were characterized by numerous thaw lakes, ponds, and basins. Wetland community types included wet sedge (*Carex* spp.) meadows, moist sedge-dwarf shrub (e.g. willow [*Salix* spp.]) meadows, and emergent sedge and pendant grass (*Arctophila fulva*) on the margins of lakes and ponds (Anderson et al. 1999). Dwarf willow was the dominant shrub and the main source of cover for nesting waterfowl.

4.3.2. Field methods

We systematically searched wetland basins on foot for King Eider nests, beginning in mid-June at both sites in all years (2002-2005). We searched a larger area at Kuparuk (Kuparuk approx. 1,500 ha; Teshekpuk approx. 1,000 ha) because a road system facilitated access there. We marked nests with a tongue depressor placed 1 m from the nest in vegetation, so as to be concealed from potential nest predators, and recorded latitude and longitude of each nest using a hand-held Global Positioning System (GPS) unit. We calculated nest-initiation dates by either backdating from known laying dates or from estimating incubation stages by candling eggs (Weller 1956) and assuming a laying interval of one egg per day and an incubation length of 23 days (Lamothe 1973). We monitored all nests once per week. After the initial nest visit, we tried not to flush hens from their nests. We designated a successful hatch by presence of either eggshells with detached membranes (Girard 1939) or ducklings. If there were eggshells with no membranes, or if the entire clutch was absent, we considered the nest depredated.

We classified nest sites as island or mainland after most nests had hatched; we defined islands as sites where we had to cross any depth and distance of water to reach them. Water levels tended to drop during the season and some nest sites that were islands during initiation of nest building were mainland at hatch. However, this only affected very shallow water islands where it was questionable if water level provided any protection at any point in the season. We recorded percent cover by willow within 1 m of the nest after hatch.

We placed data loggers (HOBO-TEMP, Onset Computer Corporation) opportunistically in nests at Teshekpuk (n = 36) and Kuparuk (n = 30) and programmed them to record nest temperature every 2 minutes. We used blown chicken eggs, dyed olive green and attached to a bolt, to hold thermistor probes. We drove the bolt into the ground under the nest, anchoring the probe and dummy egg in the nest (see Quakenbush et al. 2004), which allowed for a quick response to any change in temperature because the probe had only an eggshell between it and the incubating female. We defined incubation constancy as the percentage of time the female was on her nest over the period of days for which we had data. All aspects of the field work were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (UAF IACUC 05-29-King Eider).

4.3.3. Data analysis

Site characteristics.- We used general linear models to evaluate factors influencing percent willow within 1 m of the nest (willow) using 3 a priori candidate models with variables site and island or mainland location ($Willow_{site}$, $Willow_{island}$, $Willow_{island,site}$). Similarly we evaluated factors influencing initiation of egg-laying using 3 a priori candidate models with variables site and year ($Initiation_{site}$, $Initiation_{year}$, $Initiation_{site, year}$). We selected the best approximating models using Akaike's Information Criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002).

Modeling daily nest-survival rate - We evaluated competing biologically relevant, models of daily survival rate (DSR) of nests using generalized nonlinear mixed models

(Rotella et al. 2004, Stephens et al. 2005). We used PROC NLMIXED in SAS as described by Rotella et al. (2004) because it allowed us to model our binomially distributed data and consider the effects of both time-varying and time-invariant covariates on nest survival (SAS Institute, Cary, North Carolina). We modeled the relationships between DSR and covariates with a logit link function (see Stephens et al. 2005) and selected the best approximating models using AIC_c (Burnham and Anderson 2002). We present the odds ratios and their 95% confidence intervals as a measure of the effect size of the variables in our models. Odds ratios = 1.0 imply no survival differences, and therefore odds-ratio confidence intervals that include 1.0 indicate that the covariate does not significantly affect survival. For example, an odds ratio of 0.80 for the comparison of nest survival on islands versus mainland indicates that the odds of nest survival on islands were 20% lower than nest survival on the mainland (Corcoran et al. 2007).

We back-transformed logit-scale regression equations to get real DSR estimates, and we obtained period-specific survival as the product of the age specific DSR estimates. We used a period length of 27 days: 23 days of incubation (Lamothe 1973) and 4 days of laying (average 4 egg clutch; one egg laid/day). We approximated variance of overall nest survival using bootstrapping simulation (Efron and Tibshirani 1993). We produced 1000 bootstrapped-resamples of the original data set (i.e., resampling nests with replacement, up to the original sample size within each site-year; PROC SURVEYSELECT) and estimated nest survival for each using the best approximating model. We used the standard deviation among the 1000 bootstrapped estimates (for each

site yr) as the standard error for overall nest survival in each site-year (Efron and Tibshirani 1993). We estimated spatio-temporal process variation in nest survival using variance-components approaches outlined by Burnham et al. (1987: 260). We used the variance among the 1000 bootstrapped nest survival estimates as our estimate of sampling variance within a given site-year.

We model-averaged parameter estimates (θ) and associated variances from the candidate model set (Burnham and Anderson 2002). Additionally, we reported odds ratios of the model-averaged parameter estimates and their 95% confidence intervals. We calculated relative importance of each predictor variable as the sum of Akaike weights across all models in the set where the variable occurred (Burnham and Anderson 2002). We report values as mean ± standard error.

Model justification and prediction.- We investigated 3 candidate model sets; the first to investigate ecological factors influencing nest survival of King Eiders on the coastal plain of northern Alaska, the second to estimate nest survival, sampling error, and process error, and the third to investigate the effect of incubation constancy on nest survival using a subset of the data. We used a multiple model set approach so that we could investigate ecological questions using a complex set of models that could potentially make nest survival estimation difficult or impossible (e.g. Dinsmore et al. 2002). Further, separate nest survival estimates for sites and years are important for future population modeling and may not be a product of the top model from the ecological factors model set.

The first model set included 15 a priori models that examined effects of year, site, daily nest age, a time trend, observer effects, and 2 covariates; island or mainland nest location (island), and percent willow within 1 m of the nest (willow). Our simplest model was that of constant daily survival (model no. 1); we then modeled the main effects of site (no. 2) and year (no. 3) separately. The DSR may vary across the nesting season (time trend) if external factors such as weather or available forage vary predictably across the season. The DSR may also increase with age of the nest (age) as the reproductive value of the attempt increases, or due to nests with inherently lower survival probabilities being less likely to persist in the sample as incubation progresses. Therefore, for each of these 2 main-effects models, we fit 3 additional additive models, one with a linear trend through time within the season on daily nest survival (no. 4, no. 7), one with nest age effects (no. 5, no. 8), and a third with both (no. 6, no. 9). The DSR may be higher on islands as females may derive some protection from mammalian egg predators there (secluded strategy) or higher at nests with more cover (concealed strategy). We modeled effects of 2 covariates (island and willow) by adding each one separately (no. 10, no. 12) to the best model (DSR_{site}) from the set of 9 models that we had run thus far and then included an interaction with the main effect in the model (no. 11, no. 13). Our small data set limited the number of models we could investigate (Burnham and Anderson 2002), so we added these covariates in a hierarchical manner (Langtimm et al. 1998, Stephens et al. 2005). Additionally, we included an interaction with site, year, and island in one model because there was fox control in 2005 at the Kuparuk study area, which could have influenced the effect of islands in that year (no. 14).

Researchers typically visit nests periodically to determine nest success, sometimes displacing birds off their nests in the process (Mayfield 1975). Disturbance associated with regular nest visits may affect success of those nests under observation (i.e. observer effect; Bart 1977, Mayer-Gross et al. 1977, Bart and Robson 1982, Rotella et al. 2000, Lloyd and Plagány 2002). Observer effect may be caused by exposing the nest to predation following displacement of the parents or by attracting or repelling predators (reviewed by Götmark 1992). Because small changes in DSR translate into large changes in nest success, small observer effects can strongly affect estimates of nesting success and may even yield misleading conclusions regarding population viability (Rotella et al. 2000). Specifically, we created an index variable that took the value of one on the first day of the interval after the nest was visited and zero otherwise (Rotella et al. 2000). We then used this variable to evaluate whether there was an effect on daily survival rates the day following a nest visit by adding it to the best model (DSR_{site}; no. 15).

After the initial a priori model selection process, we built 2 exploratory models with an interaction between observer effect in the best model and island ($DSR_{site, observer, island, observer \times island}$) and willow ($DSR_{site, observer, willow, observer \times willow}$) and a third that considered effects of both island and willow ($DSR_{site, island, willow}$).

The second a priori candidate model set considered each site year separately and included models with additive and multiplicative effects of initiation of laying (init) and nest age (age) on daily nest survival. As observer effects were important in the first model set, we built an exploratory model that included an additive observer effect to the

top a priori model. We used the top models before and after the inclusion of the exploratory model to estimate daily nest survival, period-specific survival, sampling variances and process error among site years. We estimated observer-related reductions to nest survival by calculating nest survival from both DSR models in which observer effects were accounted for (via model structure), but not included in back-transformation calculations, and nest survival from models in which observer effects were unseparated from natural mortality (i.e., no observer effect term in the model; Wilson 2007).

The third a priori candidate model set considered a subset of the data to evaluate the effect of incubation constancy on daily nest survival. We did not have estimates of incubation constancy for all nests in the first model set, forcing us to employ this additional exercise in model selection. This model set included the top model from the first model set, constant daily survival, and an additive effect of incubation constancy on both previous models.

4.4. Results

We monitored 289 King Eider nests over 4 years. Annual number of nests ranged from 30-42 at Kuparuk and 33-42 at Teshekpuk. Initiation of egg-laying varied between sites; the top model of the candidate model set ($Initiation_{site}$; $AIC_c = 692.76$, AIC_c wt= 0.80) was 3.39 AIC_c units from the next best model ($Initiation_{site, year}$). Parameter estimates (effect sizes, θ) from the top model indicated that initiation was later at Teshekpuk than Kuparuk ($\theta_{site} = -1.48$, 95% CI = -2.91– -0.05). On average, females at Kuparuk initiated egg-laying on 17 June and at Teshekpuk on 19 June. First nests were initiated the first

week in June each year and egg laying continued through the end of June (Fig. 4.1). We observed arctic fox, glaucous gulls (*L. hyperboreus*), and parasitic (*S. parasiticus*) and long-tailed (*S. longicaudus*) jaegers depredating nests. Ravens and red fox (*Vulpes vulpes*) were also present in the study areas.

The top model of the candidate model set describing percent willow within 1 m of the nest ($Willow_{site, island}$; AIC_c = -1001.27) was 2.84 AIC_c units from the next best model ($Willow_{site}$) and carried 81% of the AIC_c weight. Percent willow ranged from 0-95% and differed between sites (θ_{site} = -0.09, 95% CI = -0.13– -0.05); Teshekpuk had on average double the amount of willow (18.1% ± 2.3) than did Kuparuk (9.0% ± 0.8). Overall, most (95%) nests had <50% cover by willow, and nests on islands had more willow (θ_{island} = -0.05, 95% CI = -0.09– -0.01) than did mainland nests. Proportions of nests on islands were similar between the 2 sites (Kuparuk, 50%; Teshekpuk, 55%).

The best approximating a priori model describing ecological factors influencing King Eider nest success included effects of site and observer ($DSR_{site, observer}$) and was 3.37 AIC_c units from the next best model (DSR_{site}). All models within 7 AIC_c units of the top model included effects of site (Table 4.1). The best approximating model indicated that the odds of nest survival were 40% lower at Teshekpuk than Kuparuk (β_{site}= -0.5, 95% CI = -0.8– -0.2; odds ratio = 0.6, 95% CI = 0.4–0.8) and 60% higher on days when nests were not revisited ($\beta_{observer}$= -0.9, 95% CI = -1.7– -0.2; odds ratio = 0.4, 95% CI = 0.2–0.9).

Including the 3 exploratory models changed the ranking of the top models. The exploratory model $DSR_{site, observer, observer \times willow}$ was the top ranked model when included and was 5.17 AIC_c units from the next best model ($DSR_{site, observer}$), the top a priori model. The exploratory models $DSR_{site, observer, island, observer \times island}$ and $DSR_{site, island, willow}$ were 8.04 and 11.13 AIC_c units from the top model ($DSR_{site, observer, willow, observer \times willow}$), respectively. The best approximating exploratory model indicated that DSR was higher at Kuparuk than Teshekpuk (β_{site}= -0.5, 95% CI = -0.8– -0.1; odds ratio = 0.6, 95% CI = 0.4–0.9) and that there was an effect of willow cover in concert with an observer effect. Nest survival was lower at nests with a higher percentage of cover from willow on days when nests were not revisited (β_{willow}= -1.8, 95% CI = -0.5– -3.1; odds ratio = 0.2, 95% CI = 0.1–0.6), but higher on days when the nest was visited ($\beta_{observer \times willow}$= 6.1, 95% CI = 2.3–10.0; odds ratio = 465.4, 95% CI = 9.8–22,057.3; Fig. 4.2), although this effect size was poorly estimated. Model-averaged odds ratios indicated that nest survival decreased as willow cover increased and was higher at Kuparuk and on days when the nest was not visited (Table 4.2). There was little support for the parameters island, nest age, and time trend, and model-averaged odds ratios indicated no effect (Table 4.2). The exploratory model including an interaction between observer and island had little support and the interaction was imprecisely estimated ($\beta_{observer \times island}$= -0.2, 95% CI = -1.7–1.3; odds ratio = 0.8, 95% CI = 0.2–3.6).

The top a priori model from the candidate model set for estimation of nest survival, $DSR_{site, year, age, site \times year, site \times age, year \times age}$, was 2.33 AIC_c units from the next best model (Table 4.3). Daily nest survival varied among site years and with age of the nest;

however all odds ratios 95% confidence intervals overlapped one, indicating no effect. The exploratory model $DSR_{site, year, age, site \times year, site \times age, year \times age, observer}$ (AIC_c = 799.76, AIC_c weight = 0.79) was a 3.85 AIC_c improvement on the top a priori model. Daily nest survival was lower when visited by an observer ($\beta_{observer}$ = -1.03, 95% CI = -1.91– -0.16; odds ratio = 0.36, 95% CI = 0.15–0.85), as we found in the first model set. Nest survival ranged from 0.12 - 0.26 at Teshekpuk and 0.10-0.43 at Kuparuk when the observer effect was not accounted for (i.e. no observer effect term in model). Nest survival estimated from the model controlling for an observer effect via model structure was much higher, 0.22 - 0.40 at Teshekpuk and 0.21 - 0.57 at Kuparuk (Table 4.4). Estimated site year-specific process variation in DSR was 0.010 (95% CI = 0.007–0.075; $DSR_{site, year, age, site \times year, site \times age, year \times age}$). Estimated site year-specific process variation using the exploratory model $DSR_{site, year, age, site \times year, site \times age, year \times age, observer}$ was 0.007 (95% CI = 0.003–0.070).

We did not find an effect of incubation constancy on nest survival. Addition of the constancy variable added 2 AIC_c units but did not change deviance (Table 4.5). Odds of nest survival increased 2.1-fold for each unit increase in constancy, however the estimated effect was imprecise ($\beta_{constancy}$ = 0.73, 95% CI = -7.9–9.4; odds ratio= 2.1, 95% CI = -0.00–11,118.5).

4.5. Discussion

King Eiders breeding on the coastal plain of northern Alaska over the 4 years of our study experienced somewhat higher nest success (21-57%) than reported for King Eiders nesting in the high arctic (0-21%; Lamothe 1973). However, semi-colonial, island-

nesting King Eiders in Nunavut, Canada had higher nest success (30-89%; Kellet et al. 2003), presumably due to the benefits of nesting on isolated islands. Our estimates were within the range reported for common (*S. mollissima*; Spitzbergen 27-93%, Ahlén and Andersson 1970; Beaufort Sea, AK 33%, Schamel 1977) and spectacled eiders (*S. fischeri;* Western Alaska 18-76%, Grand and Flint 1997; Arctic Russia 2-30%, Pearce et al. 1998). Nest survival for King Eiders was highly variable on both temporal and spatial scales on the coastal plain of northern Alaska. However, process variance was low, indicating that most variance was from sampling, potentially due to our small sample size.

We found mixed support for the concealed breeding strategy, possibly due to King Eiders being caught between competing selection pressures associated with avian and mammalian egg predation. To avoid avian predation it should be advantageous to nest in areas with willow cover, as nests are less likely to be detected both when attended and unattended. Evidence for this benefit can be seen in the decreasing observer effect as willow cover increases. The primary source of nest loss associated with observer effects is likely avian predators taking advantage of exposed nests (Bolduc and Guillemette 2003). However, in the absence of observers, nest success was actually lower at nest sites with more cover from willow. This negative effect of cover may be a reflection of an unmodeled variable that was correlated with percent willow (e.g. distance to water) or to different predators being responsible for observer-induced mortality. Although foxes are unlikely to be actively searching for King Eider nests because nests occur in such low densities in our study area, foxes may focus on foraging in areas with willow cover as the

most efficient habitat for them to hunt, increasing their likelihood of approaching prey undetected or because prey densities are generally higher in these habitats. Thus, the overall negative association between nest survival and willow cover may actually be driven by fox predation. We argue that selection of willow cover is an adaptation to avoid avian predation and that nest habitat selection by King Eider may have evolved in the absence of heavy fox predation, resulting in an ineffective strategy at current fox population levels. It is important to remember that we drew these conclusions from an exploratory model and they should be viewed with caution; more research is needed to explore competing selection pressures associated with predation pressure.

King Eiders did not have increased nest success on islands, contrary to our predictions regarding avoidance of mammalian predation. Our definition of islands included those in very shallow water, which is unlikely to offer much deterrent to mammalian predators and may have contributed to the lack of finding an effect. Kellett et al. (2003) found that King Eiders had greater nest success on more isolated islands (farther from the mainland) and their exclusively island-nesting population at Karrak Lake experienced much higher success (30-89%) than reported for mainland populations (0-56%; Lamothe 1973, this study). However, the islands at Karrak Lake were much larger and in deeper water, and likely provided more complete protection than the islands in shallow water tundra ponds that characterize much of the King Eiders' circumpolar breeding areas. Further, the Karrak Lake eiders are nesting within a large lesser snow (*Chen caerulescens*) and Ross' goose (*C. rossii*) colony, which could provide a buffer from predators. King Eiders nesting in areas without deep water islands may not have a

viable option for secluded nesting. Low densities of both nesting King Eiders and foxes may be required for successful breeding in absence of secluded nest sites.

It has been suggested that King Eiders nest in association with jaegers (Lamothe 1973, Blomqvist and Elander 1988), gulls (Götmark and Åhlund 1988), and terns (*Sterna paradisaea*; Kellet and Alisauskas 1997) to take advantage of the defensive behavior of these species toward shared nest predators. However, King Eiders nesting at Kuparuk and Teshekpuk appeared to avoid nesting near gulls; the average distance to the closest glaucous gull nests was 0.5 – 1.0 km (R. L. Bentzen, University of Alaska Fairbanks, unpublished data), well beyond the reported range for receiving secondary protection (Schamel 1977, Götmark and Åhlund 1988). Further, glaucous gulls are unable to repel foxes from their territories (P. Flint, unpublished data) suggesting that only avian predation pressures would be alleviated through associations with gulls. Similarly, we found no evidence of cooperation with nesting conspecifics to take advantage of their defense behaviors; King Eiders in our study sites were dispersed across the landscape, averaging 477 m (± 31.2 m) between nests.

Nest success was higher at Kuparuk than Teshekpuk; sites distant enough to be considered independent (approx. 160 km) and which differ in a variety of ways. For one, Kuparuk was within an area that has been developed for oil and gas extraction. Effects of development on animal populations include increased densities of predators in oilfields, mainly due to anthropogenic food sources (Eberhardt et al. 1982, Truett et al. 1997, Burgess 2000). These predators (foxes, gulls, jaegers and ravens) prey on eggs, nestlings

and fledglings of many birds, including King Eiders (Larson 1960, Lamothe 1973, Kellett and Alisauskas 1997). Increased predator populations may lead to decreased nest survival of tundra nesting birds, unless predators are largely subsidized by anthropogenic food sources. It seems counter-intuitive that higher nest survival at Kuparuk is a direct result of increased predator abundances. However, it is unknown whether predator densities do actually vary between Kuparuk and Teshekpuk and to what extent they are subsidized by anthropogenic food sources. The largest difference in nest success between the 2 sites was in the summer of 2005, prior to which 41 foxes were trapped and killed at Kuparuk (C. Rea, ConocoPhillips Inc., personal communication), potentially causing the very high nest success (56%) recorded that year. However, as nest success was consistently higher at Kuparuk in all years, we do not believe the 2005 predator removal alone caused site differences.

Habitat quality may vary between the 2 sites and drive differences in nest survival. Potential differences include degree of concealment available at potential nest sites, food availability, and other microhabitat variables. There is some indication that King Eiders had higher food availability because their incubation breaks were shorter, yet birds lost mass at the same rate at Kuparuk (Bentzen et al. 2008). The resulting increased incubation constancy at Kuparuk may have led to increased nest success if most egg depredation occurred during incubation recesses. However, we found no relationship between incubation constancy and nest survival on the individual level, possibly due to the lack of variation in incubation constancy (making it difficult to detect an effect) or sample size or because there is no current benefit to higher versus lower incubation

constancy within the range detected. Incubation constancy varied from 70% to 100% but most females maintained constancy at 98% (R. L. Bentzen, unpublished data). King Eiders rely primarily on endogenous reserves during incubation (Lawson 2006; Bentzen et al. 2008) and have likely reduced variation in incubation constancy as much as possible, thereby limiting detrimental effects of cooling, movement to and from the nest, scent trails, and absence from the nest associated with incubation recesses. We suggest that high incubation constancy is the result of past selection but does not currently play a large role in nest survival at an individual level.

In summary, factors influencing King Eider nest success were complex. We suggest that King Eiders are caught between competing predation pressures associated with 2 primary predators, avian and mammalian. It appeared King Eiders may use a concealed breeding strategy as females seemed to derive some benefit from nesting in areas with more willow on days when the nest was visited by observers, likely due to avian predation pressures. The overall negative effect of increased cover may be driven by mammalian predators preferentially foraging in these areas. We found no evidence that King Eiders employ secluded nesting strategies or that they benefit from increased incubation constancy.

4.6. Management implications

The King Eider population has declined in recent decades (Suydam et al. 2000) and the underlying causes are unknown. King Eiders were negatively impacted by observers near the nest, although females were rarely flushed on revisits, and using nest survival

estimates without considering observer effects could result in misleading conclusions. Therefore, we recommend future studies take every precaution to limit effects of nest visits and to consider them as a possible negative bias in estimated nest survival. The highest densities of King Eiders in Alaska are within the National Petroleum Reserve-ALASKA (W. Larned, United States Fish and Wildlife Service, unpublished report) which is >87% open for oil and gas leasing (Bureau of Land Management 1998, Bureau of Land Management 2004). Future models of the impact of petroleum development on nest survival of tundra-nesting waterfowl should consider the influence of humans in the vicinity of nest.

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improved previous versions of the manuscript. We thank H. Wilson for many discussions on statistical analyses and L. Phillips for help with the initial planning and execution of this study. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the United States government.

4.8. Literature cited

Ahlén, I., and Å. Andersson. 1970. Breeding ecology of an eider population on Spitsbergen. Ornis Scandinavica 1: 83-106.

Anderson, B. A., C. B. Johnson, B. A. Cooper, L. N. Smith, and A. A. Stickney. 1999. Habitat associations of nesting spectacled eiders on the Arctic Coastal Plain of Alaska. Pages 27-59 *in* R.I. Goudie, M.R. Peterson, and G.J. Robertson, editors. Behavior and ecology of sea ducks. Canadian Wildlife Service Occasional Paper, Ottawa, Ontario, Canada.

Bart, J. 1977. Impact of human visitations on avian nesting success. Living Bird 16: 187-192.

Bart, J., and D. S. Robson. 1982. Estimating survivorship when the subjects are visited periodically. Ecology 63: 1078-1090.

Bentzen, R. L., A. N. Powell, T. D. Williams, and A. S. Kitaysky. 2008. Characterizing the nutritional strategy of incubating king eiders *Somateria spectabilis* in northern Alaska. Journal of Avian Biology 39: 683-690.

Blomqvist, S., and M. Elander. 1988. King eider (*Somateria spectabilis*) nesting in association with long-tailed skua (*Stercorarius longicaudus*). Arctic 41: 138-142.

Bolduc, F., and M. Guillemette. 2003. Human disturbance and nesting success of common eiders: interaction between visitors and gulls. Biological Conservation 110: 77-83.

Bolduc, F., M. Guillemette, and R. D. Titman. 2005. Nesting success of common eiders *Somateria mollissima* as influenced by nest-site and female characteristics in the Gulf of the St. Lawrence. Wildlife Biology 11: 273-279.

Bureau of Land Management. 1998. Record of decision for the Northeast Petroleum Reserve-Alaska integrated activity plan/environmental impact statement. U. S. Department of Interior, Bureau of Land Management, Anchorage, Alaska, USA.

Bureau of Land Management. 2004. Record of decision for the Northwest National Petroleum Reserve-Alaska integrated activity plan/environmental impact statement. U. S. Department of Interior, Bureau of Land Management, Anchorage, Alaska, USA.

Burgess, R. M. 2000. Arctic fox. Pages 159-178 *in* J. C. Truett and S. R. Johnson, editors. The natural history of an arctic oil field: Development and the biota. Academic Press, San Diego, California, USA.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and analysis methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Second edition. Springer-Verlag, New York, New York, USA.

Corcoran, R. M., J. R. Lovvorn, M. R. Bertram, and M. T. Vivion. 2007. Lesser scaup nest success and duckling survival on the Yukon Flats, Alaska. Journal of Wildlife Management 71: 127-134.

Dinsmore, S. J., G. C. White, and F. L. Knopf. 2002. Advanced techniques for modeling avian nest survival. Ecology 83: 3476-3488.

Eberhardt, L. E., W. C. Hanson, J. L. Bengtson, R. A. Garrott, and E. E. Hanson. 1982. Arctic fox home range characteristics in an oil-development area. Journal of Wildlife Management 46: 183-190.

Efron, B. and R. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York, New York, USA.

Flint, P. L., J. B. Grand, T. F. Fondell, and J. A. Morse. 2006. Population dynamics of greater scaup breeding on the Yukon-Kuskokwim delta, Alaska. Wildlife Monographs 162.

Girard, G. L. 1939. Notes on the life history of the shoveler. Transactions of the North American Wildlife Conference 4: 364-371.

Götmark, F. 1992. The effects of investigator disturbance on nesting birds. Current Ornithology 9: 63-104.

Götmark, F., and M. Åhlund. 1988. Nest predation and nest site selection among eiders *Somateria mollissima*: the influence of gulls. Ibis 130: 111-123.

Goudie, R. I., G. J. Robertson, and A. Reed. 2000. Common eider (*Somateria mollissima*). Account 546 *in* A. Poole and F. Gill, editors. The Birds of North

America, The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.

Grand, J. B., and P. L. Flint. 1997. Productivity of nesting spectacled eiders on the Lower Kashunak River, Alaska. Condor 99: 926-932.

Hoekman, S. T., L. S. Mills, D. W. Howerter, J. H. Devries, and I. J. Ball. 2002. Sensitivity analyses of the life cycle of midcontinent mallards. Journal of Wildlife Management 66: 883-900.

Kellett, D. K. 1999. Causes and consequences of variation in nest success of king eiders (*Somateria spectabilis*) at Karrak Lake, Northwest Territories. Thesis, University of Saskatchewan, Saskatoon, Canada.

Kellett, D. K., and R. T. Alisauskas. 1997. Breeding biology of king eiders nesting on Karrak Lake, Northwest Territories. Arctic 50: 47-54.

Kellett, D. K., R. T. Alisauskas, and K. R. Mehl. 2003. Nest-site selection, interspecific associations, and nest success of king eiders. Condor 105: 373-378.

Langtimm, C. A., T. J. O'Shea, R. Pradel, and C. A. Beck. 1998. Estimates of annual survival probabilities for adult Florida manatees (*Trichechus manatus latirostris*). Ecology 79: 981-997.

Lamothe, P. 1973. Biology of the king eider (*Somateria spectabilis*) in a freshwater breeding area on Bathurst Island, N.W.T. Thesis, University of Alberta, Edmonton, Canada.

Larson, S. 1960. On the influence of the arctic fox *Alopex lagopus* on the distribution of arctic birds. Oikos 11: 276-305.

Lawson, S. 2006. Comparative reproductive strategies between long-tailed ducks and king eiders at Karrak Lake, Nunavut: Use of energy resources during the nesting season. Thesis, University of Saskatchewan, Saskatoon, Canada

Lloyd, P. and E. E. Plagány. 2002. Correcting observer effect bias in estimates of nesting success of a coastal bird, the white-fronted plover *Charadrius marginatus*. Bird Study 49: 124-130.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. Ecological Monographs 65: 101-127.

Mayer-Gross, H., H. Q. P. Crick, and J. J. D. Greenwood. 1977. The effect of observers visiting the nests of passerines: an experimental study. Bird Study 44: 53-65.

Mayfield, H. F. 1975. Suggestions for calculating nest success. Wilson Bulletin 87: 456-466.

Milne, H. 1976. Body weights and carcass composition of the common eider. Wildfowl 27: 115-122.

Parmelee, D. F., H. A. Stephens, and R. H. Schmidt. 1967. The birds of southeastern Victoria Island and adjacent small islands. National Museum of Canada Bulletin 222, Ottawa, Ontario, Canada.

Pearce, J. M., D. Esler, and A. G. Degtyarev. 1998. Nesting ecology of spectacled eiders *Somateria fischeri* on the Indigirka River Delta, Russia. Wildfowl 49: 110-123.

Petersen, M. R., J. B. Grand, and C. P. Dau. 2000. Spectacled eider (*Somateria fischeri*). Account 547 *in* A. Poole and F. Gill, editors. The Birds of North America, The Academy of Natural Sciences, Philadelphia, Pennsylvania, and The American Ornithologists' Union, Washington, D.C., USA.

Quakenbush, L., R. Suydam, T. Obritschkewitsch, and M. Deering. 2004. Breeding biology of Steller's eiders (*Polysticta stelleri*) near Barrow, Alaska, 1991-99. Arctic 57: 166-182.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9: 1–48.

Ricklefs, R. E. 1984. Variation in the size and composition of eggs of the European starling. Condor 86: 1-6.

Rotella, J. J., M. L. Taper, and A. J. Hansen. 2000. Correcting nesting-success estimates for observer effects: maximum-likelihood estimates of daily survival rates with reduced bias. Auk 117: 92-109.

Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. Animal Biodiversity and Conservation 27: 187-205.

Schamel, D. 1977. Breeding of the common eider (*Somateria mollissima*) on the Beaufort Sea Coast of Alaska. Condor 79: 478-485.

Stephens, S. E., J. J. Rotella, M. S. Lindberg, M. L. Taper, and J. K. Ringelman. 2005. Duck nest survival in the Missouri Coteau of North Dakota: landscape effects at multiple spatial scales. Ecological Applications 15: 2137-2149.

Suydam, R. S., D. L. Dickson, J. B. Fadely, and L. T. Quakenbush. 2000. Population declines of king and common eiders of the Beaufort Sea. Condor 102: 219-222.

Swennen, C., J. C. H. Ursem, and P. Duiven. 1993. Determinate laying and egg attendance in common eiders. Ornis Scandinavica 24: 48-52.

Truett, J. C., M. E. Miller, and K. Kertell. 1997. Effects of arctic Alaska oil development on brant and snow geese. Arctic 50: 138-146.

Weller, M. W. 1956. A simple field candler for waterfowl eggs. Journal of Wildlife Management 20: 111-113.

Wilson, H. M. 2007. Population ecology of pacific common eiders on the Yukon-Kuskokwim Delta, Alaska. Dissertation, University of Alaska, Fairbanks, USA.

Table 4.1. A priori models of daily survival rate (DSR) of King Eider nests found at Teshekpuk and Kuparuk, Alaska, 2002-2005. Factors in models included year, site, island or mainland nest location (island), logit-linear trends with time (time trend), daily nest age (age), percent of willow within 1 m of nest bowl (willow), and an observer effect.

DSR model	K[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	Deviance
Site, observer	3	801.65	0	0.54	795.64
Site	2	805.02	3.37	0.1	801.02
Site, age	3	805.66	4.01	0.07	799.65
Site, island	3	805.89	4.23	0.07	799.88
Site, time trend	3	806.04	4.38	0.06	800.03
Site, willow	3	806.89	5.24	0.04	800.88
Site, time trend, age	4	807.66	6.01	0.03	799.64
Site, island, site × island	4	807.73	6.07	0.03	799.71
Site, island, yr, site × island, yr × island	10	807.95	6.3	0.02	787.87
Site, willow, site × willow	4	808.44	6.79	0.02	800.43
Yr	4	810.96	9.31	0.01	802.94
(.)	1	811.04	9.39	0.01	809.04
Yr, age	5	811.21	9.55	0.01	801.18
Yr, time trend	5	811.24	9.59	0.01	801.22
Yr, time trend, age	6	813.04	11.39	0	801.01

[a] No. of parameters in the model

[b] Akaike Information Criterion adjusted for small sample size

[c] Difference between model AIC_c and AIC_c value of the best model

[d] AIC_c wt

Table 4.2. Model-averaged parameters (θ), odds ratios and associated 95% confidence intervals for explanatory variables from the set of a priori and exploratory models of King Eider daily nest survival. Calculated from 289 females nesting at Teshekpuk and Kuparuk, Alaska, 2002-2005.

Variable		θ-hat	θ-hat 95% CI	Odds ratio	Odds ratio 95% CI	Relative importance[a]
Site		-0.476	-0.808, -0.144	0.621	0.446, 0.866	0.997
Observer		-1.694	-2.591, -0.796	0.184	0.075, 0.451	0.942
Willow		-1.534	-2.677, -0.402	0.216	0.069, 0.669	0.872
Island		0.008	-0.009, 0.026	1.008	0.991, 1.026	0.032
Age		0	0.000, 0.001	1	1.000. 1.001	0.013
Time trend		0	0.000. 0.000	1	1.000, 1.000	0.011
Yr[b]	2003	0.001	-0.002, 0.004	1.001	0.998, 1.004	0.006
	2004	-0.001	-0.004, 0.002	0.999	0.996, 1.002	0.006
	2005	0.002	-0.001, 0.005	1.002	0.999, 1.005	0.006

[a] Variables are not represented equally in the model set

[b] Parameter estimates for yr are relative to 2002.

Table 4.3. Model selection results for estimation of nest survival of King Eiders. Calculated from nests found at Teshekpuk and Kuparuk, Alaska, 2002-2005. Factors in models included year (yr), site, daily nest age (age), and initiation date (init).

DSR[a] model	K[b]	AIC_c[c]	ΔAIC_c[d]	w_i[e]	Deviance
Site, yr, age, site × yr, site × age, yr × age	13	803.61	0	0.56	777.48
Site, yr, init, age, site × yr, site × init, yr × init, site × age, yr × age	18	805.94	2.33	0.17	769.68
Site, yr, site × yr	8	807.38	3.77	0.09	791.33
Site, yr, init, site × yr	9	807.46	3.85	0.08	789.39
Site, yr, age, site × yr	9	808.08	4.47	0.06	790.01
Site, yr, init, site × yr, site × init, yr × init	13	809.43	5.81	0.03	783.29
(.)	1	811.04	7.43	0.01	809.04

[a] Daily survival rate

[b] No. of parameters in the model

[c] Akaike Information Criterion adjusted for small sample size

[d] Difference between model AIC_c and AIC_c value of the best model

[e] AIC_c wt

Table 4.4. Estimates of nest survival from the top a priori and exploratory models of King Eiders at Teshekpuk and Kuparuk, Alaska, 2002-2005. The top a priori model ($DSR_{site, year, age, site \times year, site \times age, year \times age}$) does not separate observer effects from natural mortality, whereas the top exploratory model ($DSR_{site, year, age, site \times year, site \times age, year \times age, observer}$) accounted for observer effects via model structure, but we did not include these effects in back-transformation calculations, effectively estimating nest survival as though the nests were never visited.

			No observer effect		Controlled for observer effect	
Site	Yr	n[a]	Nest survival	SE	Nest survival	SE
Teshekpuk	2002	42	0.26	0.06	0.4	0.11
	2003	40	0.13	0.06	0.22	0.10
	2004	33	0.12	0.05	0.23	0.11
	2005	35	0.14	0.06	0.27	0.11
Kuparuk	2002	42	0.42	0.11	0.56	0.12
	2003	35	0.23	0.09	0.38	0.13
	2004	30	0.10	0.05	0.21	0.12
	2005	32	0.43	0.10	0.57	0.12

[a] No. of nests in each site yr.

Table 4.5. Model selection results for effect of incubation constancy on daily survival rate (DSR) of King Eider nests. Calculated from nests found at Teshekpuk and Kuparuk, Alaska, 2002-2005. Factors in models included site, observer effect, and incubation constancy.

DSR model	K[a]	AIC_c[b]	ΔAIC_c[c]	w_i[d]	Deviance
Site, observer	3	152.05	0	0.73	146.04
Site, observer, incubation constancy	4	154.03	1.98	0.27	146.02
(.)	1	162.4	10.34	0	160.39
Incubation constancy	2	164.14	12.09	0	160.14

[a] No. of parameters in the model

[b] Akaike Information Criterion adjusted for small sample size

[c] Difference between model AIC_c and AIC_c value of the best model

[d] AIC_c wt

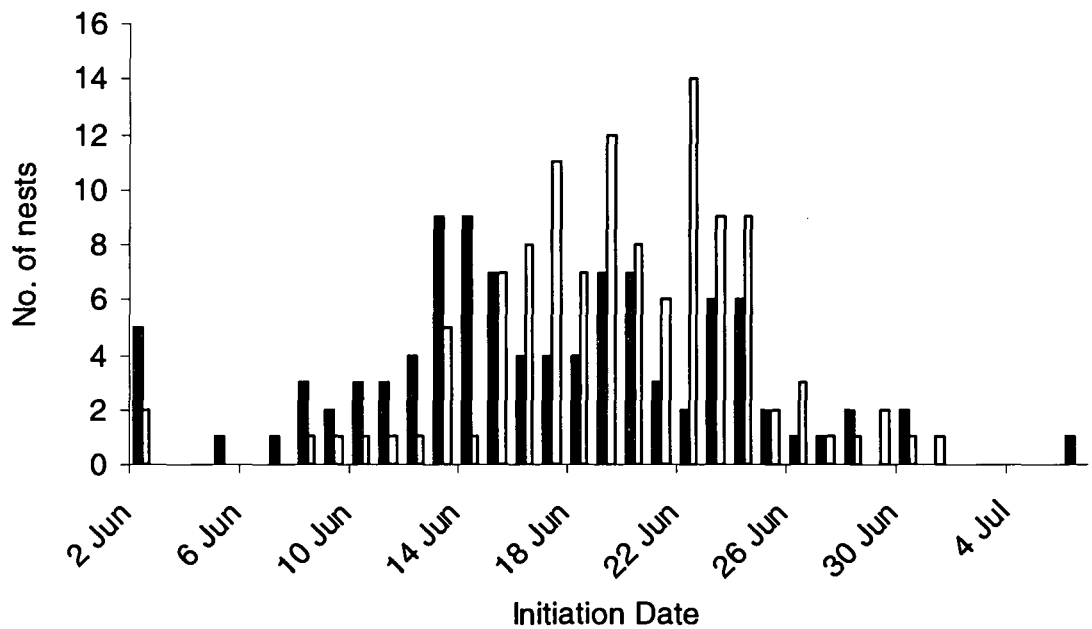

Figure 4.1. Distributions of nest initiation dates for King Eiders nesting at Teshekpuk (white bars) and Kuparuk (black bars), Alaska, 2003-2005.

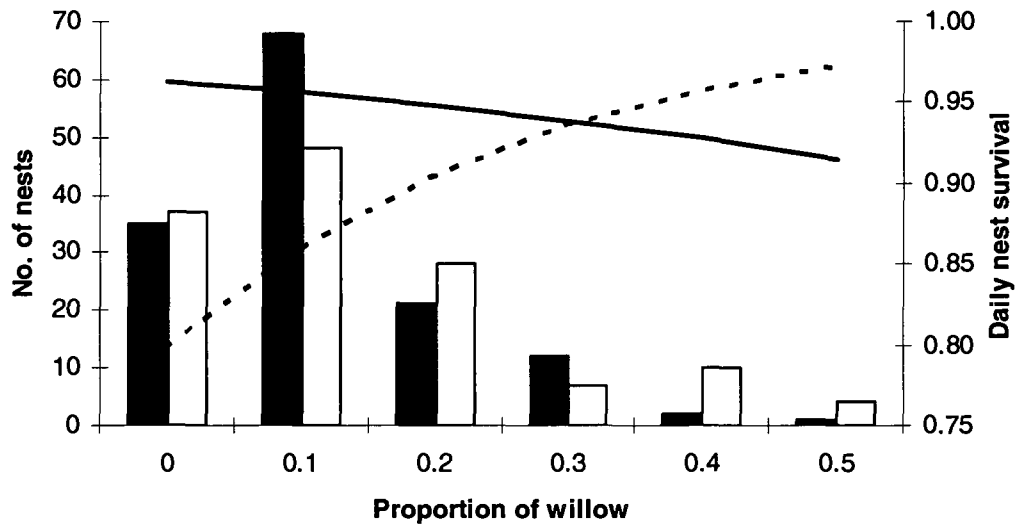

Figure 4.2. Predicted daily survival rates of King Eider nests at Teshekpuk, Alaska, 2002-2005. Calculated for the day when an observer visits (dashed line) and does not visit (solid line) in relation to the proportion of willow within one meter of the nest site. Frequency of nests at Teshekpuk (white bars) and Kuparuk (black bars), Alaska, in relation to proportion of willow within 1 m of the nest site.

5. EFFECTS OF CONCEALMENT, SECLUSION, AND NESTING ASSOCIATIONS ON NEST SITE SELECTION BY KING EIDERS [1]

5.1. Abstract

Nest site selection is a critical component of reproduction and has presumably evolved in relation to predation, local resources, and microclimate. We investigated nest site choice by King Eiders (*Somateria spectabilis*) on the coastal plain of northern Alaska, 2003-2005. We hypothesized that nest site selection is driven by predator avoidance and that a variety of strategies including concealment, seclusion, and conspecific or interspecific nest defense might lead to improved nesting success. We systematically searched wetland basins for King Eider nests and measured habitat and social variables at nests (n = 212) and random locations (n = 493). King Eiders made use of both secluded and concealed breeding strategies; logistic regression models revealed that females selected nests close to water, on islands, and in areas with high willow (*Salix* spp.) cover but did not select sites near conspecific or glaucous gull (*Larus hyperboreus*) nests. The most effective nest placement strategy may vary depending on density and types of nest predators; seclusion is likely a mammalian predator avoidance tactic whereas concealment may provide protection from avian predators. We recommend that managers in northern Alaska attempt to maintain wetland basins with islands and complex shorelines to provide potential nest sites in the vicinity of water.

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[1] Bentzen, R. L., A. N. Powell, R. S. Suydam, R. S. 2009. Effects of concealment, seclusion and nesting associations on nest site selection by king eiders. Journal of Wildlife Management 73:932-938.

5.2. Introduction

Breeding habitat selection is a critical component of reproduction in birds because it determines the environment to which the parents and eggs will be exposed for a long period of time and has presumably evolved in relation to predation, local availability of resources, and microclimate (Gloutney and Clark 1997). An individual's chance of reproductive success increases with the ability to choose a nest site that minimizes risk of predation to eggs, chicks, and attendant adults. Nest losses often constitute the greatest source of annual mortality in birds (Ricklefs 1969), and therefore any adaptations that increase nest success even slightly, such as nest site choice, should have selective value (Ricklefs 1984). Predators are the most important selective force affecting nest success (Ricklefs 1969, Martin 1995), potentially resulting in a variety of strategies related to nest protection, including breeding synchrony (Ims 1990), coloniality (Wittenburger and Hunt 1985), distraction behavior (Lack 1968, Trivers 1972), aggressive nest defense (Edmunds 1974), and nest-site selection (Larson 1960, Crabtree et al. 1988, Kellett et al. 2003).

King Eiders (*Somateria spectabilis*) typically choose nest sites that are dispersed across the tundra or on islands in tundra lakes throughout the circumpolar arctic (Kellett and Alisauskas 1997, Suydam 2000). Although little is known about King Eider nesting habitats (Suydam 2000), avoidance of predators, primarily arctic foxes (*Alopex lagopus*), may drive nest site selection (Larson 1960, Kellett et al. 2003). Larson (1960) argued that 2 main evolutionary strategies are used by arctic-nesting birds that have a limited ability to defend their nests: 1) secluded nesting, wherein success increases with greater inaccessibility of nest location, or 2) concealed nesting, wherein success increases with

more concealed nest location. In most waterfowl, and eiders in particular, the main option for secluded breeding is to nest on islands. The concealed breeding strategy relies on the nest and attendant female being camouflaged to some degree, usually by vegetation around the nest (Larson 1960).

Predators of King Eider eggs are either avian (gulls [*Larus* spp.], jaegers [*Stercorarius* spp.], and common ravens [*Corvus corax*]) or mammalian (arctic fox; Lamothe 1973, Kellett 1999) and strategies to avoid predation likely vary by predator type. Incubating eiders are unable to defend their nests from foxes and do not feign injury to draw potential predators from the nest, suggesting that eiders should benefit from secluded nesting in the presence of arctic foxes (Larson 1960). However, King Eiders have been known to successfully deter predation attempts by gulls (Kellett and Alisauskas 1997) and jaegers (Blomqvist and Elander 1988), thus most avian depredation occurs when incubating females are absent from their nests (Swennen et al. 1993). Therefore, to avoid avian predation it would be advantageous to maintain high incubation constancy and maximize nest concealment.

Nesting associations with conspecifics or other avian species may also be important to nest success. King Eiders may defend their nests either individually or in cooperation with conspecifics (Kellett and Alisauskas 1997, Blomqvist and Elander 1988). Although generally considered solitary nesters, semi-colonial nesting does occur in some locations (Kellett and Alisauskas 1997). Additionally, protection from both avian and mammalian predators may be gained by nesting in association with species that

defend their own nests aggressively (Giroux 1981, Blomqvist and Elander 1988, Kellett and Alisauskas 1997, Quakenbush et al. 2004). King Eiders sometimes nest in association with jaegers (Lamothe 1973, Blomqvist and Elander 1988), gulls (Götmark and Åhlund 1988), and terns (*Sterna paradisaea*; Kellett and Alisauskas 1997), however, the adaptive significance of these nesting associations is unclear because some of these species are also significant predators of eggs and ducklings (Dwernychuk and Boag 1972, Giroux 1981, Blomqvist and Elander 1988, Kellett and Alisauskas 1997).

The coastal plain of northern Alaska includes the entire breeding range of King Eiders within Alaska (Suydam 2000) and is representative of King Eider habitat across a larger scale. The highest densities of nesting King Eiders in Alaska are within the northeast planning area of the National Petroleum Reserve-Alaska (NPR-A; W. Larned, United States Fish and Wildlife Service, unpublished report), which is 87% open for oil and gas leasing (Bureau of Land Management 1998). Oil and gas development can have impacts ranging from habitat loss to increased predation by foxes and gulls (Eberhardt et al. 1982, Truett et al. 1997, Burgess 2000, National Research Council 2003). Nest site availability for tundra-nesting waterfowl on the coastal plain is also likely to be impacted by climate change. Knowledge of nest site selection under current conditions is vital to evaluating and managing any future changes. Our goal was to evaluate social (distance to nearest conspecific nest and distance to nearest glaucous gull [*L. hyperboreus*] nest) and habitat (distance to water, % willow [*Salix* spp.] within 1 m, and island location) variables that may influence King Eider nest site choice on the coastal plain of northern Alaska. We hypothesized that nest site selection is driven by predator avoidance (Kellett

and Alisauskas 1997, Kellett et al. 2003) and that concealment and seclusion of nests is likely to affect nest placement.

5.3. Methods

5.3.1. Study area

We studied King Eiders nesting at 2 sites on the north slope of Alaska, one near Teshekpuk Lake (153°07'W, 70°25'N) and another within the Kuparuk oilfields (149°41'W, 70°27'N), 2003-2005 (Fig. 5.1). The Teshekpuk site was approximately 10 km south of the southeast shore of Teshekpuk Lake in the northeast planning area of the NPR-A and experienced minimal human impact (i.e. no roads, communities, or development for petroleum extraction). The Kuparuk study site was between the Colville and Kuparuk river deltas, within a site developed for petroleum production, and had associated road networks and human activities. Both study sites were characterized by numerous thaw lakes, ponds, and basins. Wetland community types included wet sedge (*Carex* spp.) meadows, moist sedge-dwarf shrub (e.g. willow) meadows, and emergent sedge (*Carex* spp.) and pendant grass (*Arctophila fulva*) on the margins of lakes and ponds (Anderson et al. 1999). Dwarf willow (<40 cm in ht) was the dominant shrub and the main source of cover for nesting waterfowl.

5.3.2. Field methods

Habitat selection analysis can be greatly influenced by the extent of the study area chosen to represent available habitat (McClean et al. 1998, Huston 2002), thus we searched both study areas for eider nests in 2002, prior to this study. Based on this preliminary study,

we considered wetland basins (Jorgenson et al. 2003*a*) as available habitat for nesting King Eiders. Additionally, an earlier study done at a larger spatial scale indicated that King Eiders selected vegetation classes associated with lakes and ponds and avoided vegetation classes at well-drained sites on Alaska's coastal plain (John Payne, Ducks Unlimited Inc., unpublished data). Near Teshekpuk, wetland basins were often adjacent to each other, but ranged from 1-4 km apart at Kuparuk. In addition, we were able to search a larger area at Kuparuk (approx. 25 km^2 vs. 18 km^2 at Teshekpuk) because of road access there. We systematically searched wetland basins for King Eider nests on foot, approximately 14 June through approximately 4 July at both sites and in all years (2003-2005). We searched all wetlands at least twice to account for females that initiated later than average and because of lower nest detection probabilities during egg-laying. Edges of wetland basins were delineated by either low bluffs or dry tussock tundra. The farthest distance from water that we searched was 400 m. We marked nests with a tongue depressor placed 1 m away and concealed in vegetation. We recorded latitude and longitude of all King Eider and glaucous gull nests using a hand-held Global Positioning System (GPS) unit.

We generated random points within wetland basins using the Random Point Generator 1.3 extension for ArcView Geographic Information System (GIS). We classified nests and random locations as island or mainland after most nests had hatched (15-28 Jul). We defined islands as sites where we had to cross any depth (>5 cm) and distance of water to reach them and if the island was large enough for a King Eider nest. We recorded distance to nearest permanent water and percent cover by willow within 1 m

of nests and random locations after hatch. We calculated distances to the nearest glaucous gull and King Eider nests using the spatial join function of the Geoprocessing Wizard extension in ArcView. Wetlands were largely snow-free prior to initiation of egg laying, although deeper ponds and lakes still contained considerable ice cover, and glaucous gulls were present on their territories prior to King Eider nest initiation.

In 2004 and 2005 we visited an additional set of random locations (generated by the Random Point Generator) located in areas with a high concentration of islands, to boost the sample size of islands as random points and investigate characteristics of islands selected by King Eiders. For nests and random points located on islands, we measured island length, distance to mainland, and depth of water at the deepest point of the shallowest route between the island and the mainland. All aspects of our field work were approved by the University of Alaska Fairbanks Institutional Animal Care and Use Committee (UAF IACUC 05-29).

5.3.3. Data analysis

Because little is known about nest site selection for King Eiders, we developed 46 a priori models to investigate social and habitat factors that might influence nest site selection. Our candidate model set examined effects of distance to water (water), percent willow within 1 m (willow), distance to nearest King Eider nest (conspecific), island or mainland nest location (island), and distance to nearest glaucous gull nest (gull). We included all possible 1-, 2-, and 3-variable models using combinations of the variables to investigate social and habitat aspects of nest site selection (e.g. $model_{water}$; $model_{water + willow}$;

$model_{water + willow + conspecific}$; models no. 1-25). We hypothesized that effects of these variables may vary between sites, so we included all 2-variable additive models using combinations of the habitat and social variables and site (e.g. $model_{water + site}$; models no. 26-30) and 3-variable multiplicative models including interactions with site (e.g. $model_{water + site + water \times site}$; models no. 31-35). Additionally, nest site selection may vary between years due to variation in spring weather, predator abundance, or other unknown factors, and so we included all 2-variable additive combinations of the habitat and social variables and year (e.g. $model_{water + year}$; models no. 36-40); we did not include any interactions with the variable year to limit the number of models in the candidate model set. We included 4 models with quadratic terms for water, willow, conspecific and gull (e.g. $model_{water + water2}$; models no. 41-44) because the relationship between continuous predictor variables and nest selection may not be linear. Lastly, we included a 5-variable additive model including all habitat and social variables ($model_{water + willow + conspecific + island + gull}$; model no. 45) and the null model (model no. 46).

As a separate analysis, we developed 13 a priori models describing nesting island selection by King Eiders in 2004 and 2005. We compared characteristics of islands on which eiders nested to a random sample of islands within the study area. The candidate model set included the variables length of the island (length; index of island size), distance to the mainland (distance; index of island isolation), and depth of water (depth; index of island isolation). We examined all 1- and 2-variable models (e.g. $model_{length}$; $model_{length + distance}$; models no. 1-6), multiplicative combinations of these variables (e.g.

$model_{length + distance + length*distance}$; models no. 7-9) and quadratic terms (e.g. $model_{length + length2}$; models no. 10-12). Lastly we included a null model (model no. 13).

We used logistic regression (Allison 2000; SAS Institute, Cary, NC) to fit models and used the second-order Akaike's Information Criterion (AIC_c) to identify the most parsimonious model and predict variable importance (Burnham and Anderson 2002). We did not find any evidence of overdispersion thus we did not use a quasi-likelihood adjustment to AIC_c ($QAIC_c$). Logistic regression was an appropriate tool to analyze our use-availability study design (nests and random locations) because King Eider nests are relatively easy to spot and infrequent on the landscape; therefore we assumed available units were likely to include few undetected nests. However, nests that failed early, leaving only a swirl of dead grass, may not have been detected. Because use-availability study designs are approximately equivalent to case-control designs when use is rare (Keating and Cherry 2004, Johnson et al. 2006), we could estimate approximate odds ratios. We acknowledge that our data may not be truly independent if there was strong nest site fidelity among years. As this was an unmarked breeding population we were unable to determine whether females nested close to the previous year's nest, however, we do know they did not reuse the same nest bowl (R. L. Bentzen, University of Alaska Fairbanks, unpublished data). Modeling each year separately would decrease our sample size, so we modeled all years simultaneously but included year as a potential explanatory variable. We did not detect any multicollinearity among covariates, adjusted by the weight matrix used in the maximum likelihood algorithm (Allison 2000). We tested the

top candidate model with the Hosmer-Lemeshow goodness-of-fit test statistic to ensure model fit (Hosmer and Lemeshow 1989).

We calculated Akaike weight (w_i) for each model, representing probability of that model as the best model in the set of candidate models (Burnham and Anderson 2002). We calculated the sum of model weights ($\sum w_i$) for each variable using weights of all models that contained that variable. We used model-averaged parameter estimates and unconditional standard errors averaged over all models that contained a variable to determine the importance of that variable within the candidate set of models. We calculated odds ratios from averaged parameter estimates that represented the increase in probability of a site being used as a nest for every unit increase in the predictor variable (Allison 2000). We estimated probability of use (Manly et al. 2002) at 90% of the observed range of variables to present a range of variation relative to the true amount of variation in the data. We used model-averaged parameter estimates and held other variables at mean values. We report values as means ± SE.

5.4. Results

We assessed habitat and social variables at 212 King Eider nests and 493 random locations and at an additional 232 randomly selected islands. We found 33-34 nests per year at Kuparuk and 34-40 nests per year at Teshekpuk. The earliest nests were initiated the first week in June each year, with average laying dates of 17 June (± 0.6 days) at Kuparuk and 19 June (± 0.4 days) at Teshekpuk. We observed arctic fox, glaucous gulls, and parasitic (*S. parasiticus*) and long-tailed (*S. longicaudus*) jaegers depredating nests.

Ravens, red fox (*Vulpes vulpes*), and golden eagles (*Aquila chrysaetos*) were also present on both study areas.

Nests were closer to water (average < 7 m) and in areas with higher percentage of willow (average >11 %) than were random locations ($average_{water}$ >24 m, $average_{willow}$ <6 %). Nests and random locations were both far from the closest gull or conspecific nest (average >400 m). Of the subsample of nests and random points on islands, those at Kuparuk occurred on smaller islands (average <51 m), nearer the mainland (average <57 m), and in slightly deeper water (average >37 cm) than those at Teshekpuk ($average_{length}$ >107 m, $average_{distance}$ >124 m, $average_{depth}$ < 29 cm, Table 5.1).

The best approximating a priori model describing King Eider nest site choice included the variables water, conspecific, gull, willow, and island (AIC_c = 653.0, w_i = 0.51, no. of parameters [K] = 6), and was 0.1 AIC_c units from the next best model, which did not include conspecific or gull (AIC_c = 653.1, w_i = 0.49, K = 4). These 2 models were 39 AIC_c units from the third-best model ($model_{willow + island + conspecific}$; AIC_c = 692.0, w_i = 0.00, K = 4) and 211.1 AIC_c units from the null model (AIC_c = 864.2, w_i = 0.00, K = 1). The Hosmer and Lemeshow goodness-of-fit test indicated that variables in the top model fit the logistic model (χ^2_8 = 14.5, P = 0.07). As the top 2 models carried all the weight ($\sum w_i$ = 1.0), we effectively calculated model-averaged results from only the top 2 models. Model averaging indicated that the odds of a site being selected for a nest were 4% lower with each 1-m increase of distance to water (odds ratio = 0.96) and 6% higher with each 1% increase in willow near the nest (odds ratio = 1.06). Odds of nest site

selection increased 6.1 fold for island vs. mainland locations (odds ratio = 6.11). Although the variables conspecific and gull were included in the top model, they were not in the second best model ($\Delta AIC_c = 0.1$), and odds of a site being selected for a nest did not vary for either (odds ratio = 1.00; Table 5.2). The variables site and year carried no weight (ΣAIC_c wt = 0) and did not occur in models within 66 AIC_c units of the top model, indicating that the same relationships existed across sites and years.

The best approximating model describing choice of islands for nest locations included the variables length, distance, and their interaction ($AIC_c = 312.4$, $w_i = 0.72$, K = 4) and was 3.7 AIC_c units from the next best model ($model_{length + distance}$; $AIC_c = 316.1$, $w_i = 0.11$, K = 3). The third best model was 4.4 AIC_c units from the top model ($model_{length + length2}$; $AIC_c = 316.8$, $w_i = 0.08$, K = 3); the top 3 models included 92% of combined model weights. The null model ($AIC_c = 320.2$, $w_i = 0.02$, K = 1) was only 7.8 AIC_c units from the top model. Distance to the mainland averaged 108.07 m, depth of water 32.67 cm, and island length 68.96 m on random islands across the 2 study areas. Model-averaged results indicated that estimated probability of use varied from 0.10 for a 0.5-m-long island (lower 90% observed range) to 0.27 for a 300-m-long island (upper 90% observed range). Estimated probability of use varied from 0.58 to 0.33 as distance from mainland increased from 1 m to 500 m and varied very little as depth of water increased from 5 cm to 100 cm (0.13 - 0.13; Table 5.3). Although there was some support for a quadratic effect of length, odds of an island being selected for a nest site did not vary with the quadratic term (parameter estimate <0.000, odds ratio = 1.00). The

goodness-of-fit test indicated that variables in the top model adequately fit the data (χ^2_8 = 7.5, P = 0.48).

5.5. Discussion

King Eiders selected nest sites on islands, near water, and in areas with greater willow cover, suggesting that eiders utilize strategies of concealment and seclusion. However, we found little evidence that King Eiders choose nest sites based on nesting associations with either conspecifics or glaucous gulls.

Nesting on islands is likely an avoidance tactic for mammalian predators, as islands do not provide protection from avian predators such as gulls and jaegers. At Karrak Lake, Canada, Kellett et al. (2003) found that King Eiders selected nest sites on more isolated islands (further from the mainland) and experienced higher nest success (30-89%) than reported for mainland populations in other areas (0-22%; Lamothe 1973; 21-57%, Bentzen et al. 2008). However, it was an exclusively island-nesting population, occurring within a large lesser snow (*Chen caerulescens*) and Ross's goose (*C. rossii*) colony, and islands were surrounded by relatively deep water (Kellett and Alisauskas 1997). King Eiders nesting on Alaska's coastal plain on mainland tundra and shallow-water islands did not experience higher nest survival at secluded (island) nest sites (Bentzen et al. 2008). Additionally, we did not find any preference for more isolated islands, potentially due to a lack of truly isolated islands on the coastal plain, and only weak evidence for selection of larger islands. King Eiders nesting in areas with only shallow-water tundra ponds (which characterizes much of their circumpolar range) may

not have had a viable option for secluded nesting. Without truly secluded nest sites, low densities of foxes or abundant alternative prey such as lemmings or goose eggs leading to decreased predation pressure by foxes may be required for successful breeding of eiders (Bêty et al. 2001).

King Eiders nesting on Alaska's coastal plain apparently selected for nest concealment, however, the consequences of nesting in a concealed location may be mixed. Although many studies have examined the relation between nest success and concealment, the interaction remains unclear. Some studies demonstrated a benefit (Odin 1957, Jones and Hungerford 1972, Crabtree et al. 1988), whereas others did not (Jessen et al. 1964, Dwernychuk and Boag 1972, Thorton 1982). We found that when disturbed by observers, King Eider nests with more cover had higher nest success than those nests with lower cover, likely due to avian predation while the nest was unattended; however, increased concealment at the nest actually reduced nest survival when the nest was undisturbed, potentially due to foxes focusing on foraging in areas with willow cover as the most efficient habitat for hunting (Bentzen et al. 2008).

In contrast to King Eiders nesting at other locations, eiders in northern Alaska selected sites that were very close to water (approx. 5 m); nests at Karrak Lake, Canada averaged 24 m from water (Kellett and Alisauskas 1997), whereas those at Bathurst Island, Canada, averaged 594 m from water (Lamothe 1973). Choosing a nest site close to water is not an absolute requirement for King Eiders because females can take off from land; however, it may provide either a quicker escape route or better access to food. Both

predation pressure and availability of water likely differed between the Alaskan and Canadian sites, potentially influencing nesting strategy. King Eiders studied at Karrak Lake nested exclusively on islands in deeper water (approx. 1.2 m, Kellett and Alisauskas 1997) and therefore had better protection from mammalian predators, potentially lessening the need for a quick escape route. However, eiders nesting on Bathurst Island were dispersed over open tundra with arctic fox in the vicinity (Lamothe 1973). An absence of secluded nest sites may lead to greater benefits of concealment, and nesting far from water may decrease the likelihood of fox predation if foxes target near-water habitats (Lecomte et al. 2008). As nests on islands were only slightly closer to water (2.4m ± 0.7) than those on the mainland (7.3m ± 1.4), we do not feel that selection for proximity to water is simply a by-product of strong selection for island nest sites.

Although King Eiders have been suggested to nest in association with terns (Kellett and Alisauskas 1997), jaegers (Blomqvist and Elander 1988, Lamothe 1973), and gulls (Götmark and Åhlund 1988), more recent studies have not found these associations (Kellett et al. 2003, this study). We did not find any evidence that King Eiders selected nest sites near glaucous gulls and in a parallel study found that nest survival was not affected by proximity to glaucous gull nests (R. L. Bentzen, unpublished data). A beneficial nesting association requires the aggressive nest defender initiate territory defense prior to nest selection by King Eiders and have the ability to deter other predators, while King Eiders must be able to avoid predation by their associates. Glaucous gulls were present on their territories prior to King Eider nest initiation, giving eiders the choice of association with gulls. However, jaegers and gulls eat eider eggs

(Lamothe 1973, Kellett and Alisauskas 1997), can displace eiders from their nests (R. L. Bentzen, unpublished data; P. Flint, United States Geological Survey, unpublished data), take eggs during incubation breaks (Swennen et al. 1993), and may not be able to keep arctic foxes out of their own territories (Larsen and Grundetjern 1997), thus limiting potential benefits of nesting associations to King Eiders. Nest associations reported by other researchers may have been confounded with habitat associations where both species selected the same nest habitat; social and habitat nest associations may be difficult to separate. Alternatively, in some cases nesting associations may be serendipitous in that both waterfowl and their associates may nest at high numbers or experience high nest success in years when an alternative prey, such as lemmings, are abundant. During our study, lemming populations were low and invariant (R. L. Bentzen, personal observation), possibly limiting our ability to detect beneficial nesting associations (Bêty et al. 2001).

Nest site selection did not vary between sites or among years, indicating that the same relationships existed across both variables despite some differences between study areas. The most effective nest placement strategy may vary depending on predator density and type; seclusion is likely a mammalian predator avoidance tactic whereas concealment could provide protection from both mammalian and avian predators. However, predator densities and assemblages (Callaghan et al. 2004, Pamperin et al. 2006), shrub cover (Sturm et al. 2001), and wetland configuration and formation on the coastal plain are changing (Jorgenson et al. 2003*b*, Hinzman et al. 2005), leading to unknown impacts on nest site choice and nest survival of King Eiders. Uncertainty

associated with climate change is likely to exacerbate the uncertainty in our understanding of the costs and benefits of nest site choice.

5.6. Management implications

The highest densities of King Eiders in Alaska are within the National Petroleum Reserve-Alaska (W. Larned, unpublished report), of which >87% is open for oil and gas leasing (Bureau of Land Management 1998, Bureau of Land Management 2004). To mitigate impacts of future development on eider populations, we recommend that managers on the coastal plain of northern Alaska attempt to maintain nesting habitat in wetland basins with complex structure (islands and peninsulas), thereby maximizing potential nest sites near water. Additionally, changes in breeding habitat through climate warming such as changes in shrub cover, timing of snow and ice melt, wetland hydrology, and predictability (Hinzman et al. 2005) may impact future nest site availability and nest site choice for tundra-nesting waterfowl as well as the abundance of their associated predators. We suggest that further research focusing on costs and benefits of nest site choice, and on predator-prey interactions between foxes and eiders, is vital for our understanding and ability to manage this system.

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5.8. Literature cited

Allison, P. D. 2000. Logistic regression using the SAS system: theory and application. SAS Institute, Inc., Cary, North Carolina, USA.

Anderson, B. A., C. B. Johnson, B. A. Cooper, L. N. Smith, and A. A. Stickney. 1999. Habitat associations of nesting spectacled eiders on the Arctic Coastal Plain of Alaska. Pages 27-59 *in* R.I. Goudie, M.R. Peterson, and G.J. Robertson, editors. Behavior and ecology of sea ducks. Canadian Wildlife Service Occasional Paper, Ottawa, Ontario, Canada.

Bentzen, R. L., A. N. Powell, and R. S. Suydam. 2008. Factors influencing nesting success of king eiders on northern Alaska's coastal plain. Journal of Wildlife Management 72:1781-1789.

Bêty, J., G. Gauthier, J. –F. Giroux, and E. Korpimäki. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. Oikos 93:388-400.

Blomqvist, S., and M. Elander. 1988. King eider (*Somateria spectabilis*) nesting in association with long-tailed skua (*Stercorarius longicaudus*). Arctic 41:138-142.

Bureau of Land Management. 1998. Record of decision for the Northeast Petroleum Reserve-Alaska integrated activity plan/environmental impact statement. U.S. Department of Interior, Bureau of Land Management, Anchorage, Alaska, USA.

Bureau of Land Management. 2004. Record of decision for the Northwest National Petroleum Reserve-Alaska integrated activity plan/environmental impact statement. U.S. Department of Interior, Bureau of Land Management, Anchorage, Alaska, USA.

Burgess, R. M. 2000. Arctic fox. Pages 159-178 *in* J. C. Truett and S. R. Johnson, editors. The natural history of an arctic oil field: development and the biota. Academic Press, San Diego, California, USA.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer-Verlag, New York, New York, USA.

Callaghan, T. V., L. O. Björn, Y. Chernov, T. Chapin, T. R. Christensen, B. Huntley, R. A. Ims, M. Johansson, D. Jolly, S. Jonasson, N. Matveyeva, N. Panikov, W. Oechel, G. Shaver, and H. Henttonen. 2004. Effects on the structure of Arctic ecosystems in the short- and long-term perspectives. AMBIO: A Journal of the Human Environment 33:436–447.

Crabtree, R. L., L. S. Broome, and M. L. Wolfe. 1988. Effects of habitat characteristics on gadwall nest predation and nest-selection. Journal of Wildlife Management 53:129-137.

Dwernychuk, L.W., and D. A. Boag. 1972. How vegetative cover protects duck nests from egg-eating birds. Journal of Wildlife Management 36:955-958.

Eberhardt, L. E., W. C. Hanson, J. L. Bengtson, R. A. Garrott, and E. E. Hanson. 1982. Arctic fox home range characteristics in an oil-development area. Journal of Wildlife Management 46:183-190.

Edmunds, M. 1974. Defense in animals: a survey of anti-predator defenses. Longman, London, United Kingdom.

Giroux, J. 1981. Ducks nesting in association with Canada geese. Journal of Wildlife Management 45:778-782.

Gloutney, M. L., and R. G. Clark. 1997. Nest-site selection by mallards and blue-winged teal in relation to microclimate. Auk 114:381-395.

Götmark, F., and M. Åhlund. 1988. Nest predation and nest site selection among eiders *Somateria mollissima*: the influence of gulls. Ibis 130:111-123.

Hinzman, L., N. D. Bettez, W. R. Bolton, F. S. Chapin, M. B. Dyurgerov, C. L. Fastie, B. Griffith, R. D. Hollister, A. Hope, H. P. Huntington, A. M. Jensen, G. J. Jia, T. Jorgenson, D. L. Kane, D. R. Klein, G. Kofinas, A. H. Lynch, A. H. Lloyd, A. D. McGuire, F. E. Nelson, W. C. Oechel , T. E. Osterkamp, C. H. Racine, V. E. Romanovsky, R. S. Stone, D. A. Stow, M. Sturm, C. E. Tweedie, G. L. Vourlitis,

M. D. Walker, D. A. Walker, P. J. Webber, J. Welker, K. S. Winker, and K. Yoshimkawa. 2005. Evidence and implications of recent climate change in northern Alaska and other Arctic regions. Climatic Change 72:251-98.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. John Wiley and Sons, New York, New York, USA.

Huston, M. A. 2002. Critical issues for improving predictions: introductory essay. Pages 7-21, *in* J. M. Scott, P. J. Heglund, M. L. Morrison, J. A. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson, editors. Predicting species occurrences: issues of accuracy and scale. Island Press, Washington D. C., USA.

Ims, R. A. 1990. On the adaptive value of reproductive synchrony as a predator-swamping strategy. American Naturalist 136:485-498.

Jessen, R. L., J. P. Lindmeier, and R. E. Farmes. 1964. A study of duck nesting and production as related to land use in Mahnomen County, Minnesota. Pages 26-85 *in* J. B. Moyle, editor. Ducks and land use in Minnesota. Minnesota Department of Conservation Technical Bulletin 8. St. Paul, USA.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347-357.

Jones, R. E., and K. E. Hungerford. 1972. Evaluation of nesting cover as protection from magpie predation. Journal of Wildlife Management 36:727-732.

Jorgenson, M. T., J. E. Roth, M. Emers, S. F. Schlenter, D. K. Swanson, E. R. Pullman, J. S. Mitchell, and A. A. Stickney. 2003a. An ecological land survey in the northeast planning area of the National Petroleum Reserve-Alaska, 2002. ABR, Inc., Fairbanks, Alaska, USA.

Jorgenson, T., E. Pullman, and Y. Shur. 2003b. Degradation of ice wedges in northern Alaska in response to recent warmer temperatures. SEARCH Open Science Meeting, Seattle, Washington, USA.

Keating, K. A., and S. Cherry. 2004. Use and interpretation of logistic regression in habitat-selection studies. Journal of Wildlife Management 68:774-789.

Kellett, D. K. 1999. Causes and consequences of variation in nest success of king eiders (*Somateria spectabilis*) at Karrak Lake, Northwest Territories. Thesis, University of Saskatchewan, Saskatoon, Canada.

Kellett, D. K., and R. T. Alisauskas. 1997. Breeding biology of king eiders nesting on Karrak Lake, Northwest Territories. Arctic 50:47-54.

Kellett, D. K., R. T. Alisauskas, and K. R. Mehl. 2003. Nest-site selection, interspecific associations, and nest success of king eiders. Condor 105:373-378.

Lack, D. 1968. Ecological adaptations for breeding in birds. Methuen and Co., Ltd. London, United Kingdom.

Lamothe, P. 1973. Biology of the king eider (*Somateria spectabilis*) in a freshwater breeding area on Bathurst Island, N.W.T. Thesis, University of Alberta, Edmonton, Canada.

Larsen, T., and S. Grundetjern. 1997. Optimal choice of neighbor: predator protection among tundra birds. Journal of Avian Biology 28:303-308.

Larson, S. 1960. On the influence of the arctic fox *Alopex lagopus* on the distribution of arctic birds. Oikos 11:276-305.

Lecomte, N., V. Careau, G. Gauthier, and J. –F. Giroux. 2008. Predator behavior and predation risk in the heterogeneous arctic environment. Journal of Animal Ecology 77:439-447.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic, Dordrecht, The Netherlands.

Martin, T. E. 1995. Avian life history evolution in relation to nest sites, nest predation and food. Ecological Monographs 65:101-127.

McClean, S. A., M. A. Rumble, R. M. King, and W. Baker. 1998. Evaluation of resource selection methods with different definitions of availability. Journal of Wildlife Management 62:793-801.

National Research Council. 2003. Cumulative environmental effects of oil and gas activities on Alaska's north slope. The National Academies Press, Washington, D.C., USA.

Odin, C.R. 1957. California gull predation on waterfowl. Auk 74:185-202.

Pamperin, N. J., E. H. Follmann, and B. Petersen. 2006. Interspecific killing of an arctic fox by a red fox at Prudhoe Bay, Alaska. Arctic 59:361-364.

Quakenbush, L., R. Suydam, T. Obritschkewitsch, and M. Deering. 2004. Breeding biology of Steller's eiders (*Polysticta stelleri*) near Barrow, Alaska, 1991-99. Arctic 57:166-182.

Ricklefs, R. E. 1969. An analysis of nesting mortality in birds. Smithsonian Contributions to Zoology 9:1-48.

Ricklefs, R. E. 1984. Variation in the size and composition of eggs of the European starling. Condor 86:1-6.

Sturm, M., C. Racine, and K. Tape. 2001. Increasing shrub abundance in the Arctic. Nature 411:546-547.

Suydam, R. S. 2000. King eider (*Somateria spectabilis*). Account 491 *in* A. Poole and F. Gill, editors. The Birds of North America, Inc., Philadelphia, Pennsylvania, USA.

Swennen, C., J. C. H. Ursem, and P. Duiven. 1993. Determinate laying and egg attendance in common eiders. Ornis Scandinavica 24:48-52.

Thorton, F. G. 1982. Concealment as a factor in nest site selection by seven species of Anatidae in Utah. Thesis, University of Guelph, Ontario, Canada.

Trivers, R L. 1972. The risks of avian mobbing and distraction behavior: an anecdotal review. Wilson Bulletin 102:349-352.

Truett, J. C., M. E. Miller, and K. Kertell. 1997. Effects of arctic Alaska oil development on brant and snow geese. Arctic 50:138-146.

Wittenberger, J. F., and G. L. Hunt, Jr. 1985. The adaptive significance of coloniality in birds. Pages 1-78 *in* D. S. Farner, J. R. King, and K. C. Parkes, editors. Avian Biology. Volume 8. Academic Press, Orlando, Florida, USA.

Table 5.1. Mean and standard deviation of habitat variables at King Eider nests and random locations. Calculated from variables measured at nests ($n_{Teshekpuk}$ = 112, $n_{Kuparuk}$ = 100) and random sites ($n_{Teshekpuk}$ = 214, $n_{Kuparuk}$ = 279; 2003-2005), and at island nests ($n_{Teshekpuk}$ = 36, $n_{Kuparuk}$ = 31) and random sites on islands ($n_{Teshekpuk}$ = 123, $n_{Kuparuk}$ = 109; 2004-2005) at Teshekpuk and Kuparuk, Alaska.

	Teshekpuk				Kuparuk			
	Nests		Random		Nests		Random	
Variables	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
Distance to water (m)	6.9	11.7	23.6	54.5	2.6	10.7	26.8	37.5
Willow within 1 m (%)	16.3	20.4	6.2	9.6	10.6	10.2	6.4	8.9
Nearest gull nest (m)	928.9	880.2	1,133.6	695.4	581.1	840.7	967.2	1,133.5
Nearest conspecific nest (m)	444.8	425.0	640.8	371.8	740.9	1,050.9	1,119.7	1,395.1
Island length (m)	183.4	367.3	106.5	320.4	50.6	71.7	26.6	46.8
Distance to mainland (m)	124.3	173.5	153.6	202.8	39.0	54.7	56.7	95.6
Water depth (cm)	27.1	22.9	28.5	25.5	47.9	26.6	37.3	32.6

Table 5.2. King Eider nest site selection parameter estimates. Model-averaged parameter estimates, unconditional standard errors, odds ratios, and sum of Akaike weights (Σw_i) for variables found in logistic regression models of nest site selection at Teshekpuk and Kuparuk, Alaska, 2003-2005.

Variable	Estimate	SE	Odds ratio	Σw_i
Distance to water	-0.037	0.008	0.964	1.000
% willow within 1 m of nest	0.061	0.010	1.063	1.000
Island or mainland location	1.809	0.222	6.105	1.000
Distance to conspecific nest	0.000	<0.001	1.000	0.508
Distance to glaucous gull nest	0.000	<0.001	1.000	0.508

Table 5.3. King Eider island nest site selection parameter estimates. Model-averaged parameter estimates, unconditional standard errors, odds ratios, and sum of Akaike weights (Σw_i) for variables found in logistic regression models of island nest site selection at Teshekpuk and Kuparuk, Alaska, 2004-2005.

Variable	Estimate	SE	Odds ratio	Σw_i
Island length	0.004	0.002	1.004	0.935
Distance to mainland	-0.002	0.001	0.998	0.850
Depth water	0.001	<0.001	1.000	0.051

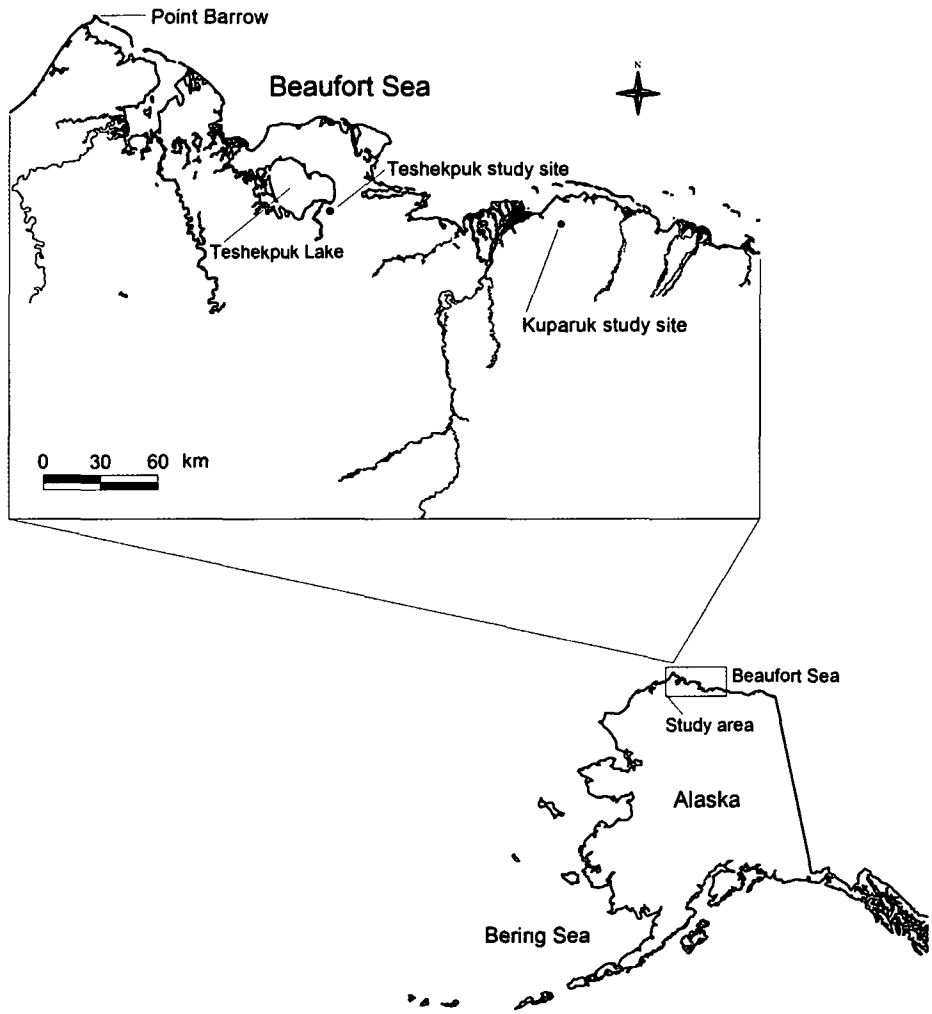

Figure 5.1. Map of the coastal plain of northern Alaska. Locations of the two study areas, Kuparuk and Teshekpuk, 2003-2005, are indicated.

6. ESTIMATING NEST SITE FIDELITY IN KING EIDERS USING MICROSATELLITE GENOTYPING; WHAT WORKED, WHAT DIDN'T AND WHY[1]

6.1. Abstract

Nest site fidelity has been well documented in female waterfowl. Fidelity to breeding areas in northern Alaska has been shown for King Eiders (*Somateria spectabilis*; Phillips and Powell 2006) but is poorly understood at a local level. We investigated local nest site fidelity and distance moved between years in relation to nest success at two remote sites on Alaska's coastal plain between 2001 and 2005. Traditional mark-recapture methods are not well suited for nesting King Eiders while genetic capture-recapture may significantly increase our ability to study site fidelity in a species that nest in low densities and experience high nest failure. We used 2 approaches to identify females; we genetically identified females from contour feathers using ten microsatellite loci, and a small number of females were trapped on their nests in late incubation and banded at both sites between 2001-2008. We found that 13 - 17% of banded females and 4% of genotyped females returned and nested in at least one year. Genotyping of contour feathers deposited in nests did not appear to be a reliable method for identifying King Eiders because a number of duplicate samples did not match. Possible causes of the inconsistent results from the genotyping include allelic dropout, recording errors, and

[1] Bentzen, R. L., A. N. Powell, L. M. Phillips, and R. S. Suydam. 2008. Estimating nest site fidelity in king eiders using microsatellite genotyping; what worked, what didn't and why. Prepared for submission in Journal of Avian Biology.

feather contamination through multiple females incubating one nest. Using only banded females, we did not detect any effect of female quality, as measured by nest success, on local fidelity. However, previously successful females that did return to the study areas nested closer to their previous nest than unsuccessful females suggesting that local familiarity influences nest site choice once the female is on the breeding grounds.

6.2. Introduction

Female waterfowl often exhibit breeding site fidelity at varying scales, which may have evolved due to the ecological advantages of site familiarity, random opportunism under certain demographic conditions, or the genetic advantages of not dispersing (see Anderson et al. 1992). Familiarity to a breeding area can increase feeding efficiency and knowledge of predator habits, and lead to improved adult, egg, and brood survival (Greenwood 1980). This has been illustrated by successful females returning to previous nest locations at a higher rate than unsuccessful females (Moran 2000, Bluhms et al. 2002). Understanding breeding area fidelity is vital to understanding local population dynamics since population growth depends not only on births and deaths, but on emigration and immigration. Additionally, philopatry and dispersal influence the genetic structure of a population (Anderson et al. 1992) and the ability to adapt to local conditions (Lack 1954).

Little is known about the breeding biology of King Eiders (*Somateria spectabilis*), partly because they typically nest in remote locations at low densities. However, the North American population has declined by more than 50% since the late 1970s (Suydam

et al. 2000, Dickson et al. 1997, Gratto-Trevor et al. 1998) for unknown reasons. Indications of decline have created an increasing interest in the ecology of King Eiders. There have been some studies dedicated to the breeding biology of King Eiders (Lamothe 1973, Cotter et al. 1997, Kellett and Alisauskas 1997, Kellett et al. 2003, Mehl et al. 2004) but many questions remain unanswered. King Eiders appear to be philopatric to their general breeding areas (Mehl et al. 2004, Kellett 1999, Phillips and Powell 2006). However, nest site fidelity at a local scale is poorly understood. Fidelity may be influenced by habitat quality around the nest, resulting in higher nest survival and a likely benefit to local familiarity if the female relies to some extent on resources obtained on the breeding grounds for reproduction. King Eider females do feed during egg production and incubation (Oppel 2008, Bentzen et al. 2008a), indicating that habitat on the breeding ground is likely important to reproductive success and that there could be a benefit to local familiarity.

Traditional mark-recapture methods are not well suited for nesting King Eiders: capture often causes abandonment, nests often fail quite early before females can be captured, leg bands cannot be read without recapture (R.L. Bentzen, University of Alaska Fairbanks, personal observation), and nasal markers can affect behavior (Brook and Clark 2002, Regehr and Rodway 2003). However, with recent improvements in molecular techniques, genetic capture-recapture may be a viable alternative. Individual identification using genetic markers such as microsatellite loci has become increasingly common, and has been used to estimate population size (Frantz et al. 2003, Fickel and

Hohmann 2006), range extent (Taberlet et al. 1997, Eggert et al. 2007), and breeding site fidelity (Fowler 2005). Non-invasive sampling, such as hair snags (Mowat and Strobeck 2000), fecal samples (Frantz et al. 2003, Eggert et al. 2007), skin biopsies (Palsbøll et al. 1997) and contour feathers (Pearce et al. 1997, Fowler 2005) can provide the genetic material for these methods, eliminating the need to physically mark or handle the animal in question. King Eiders appear to be a good candidate for this approach. Females deposit contour feathers in their nests soon after initiation and their nests are relatively easy to find, both while active and after failure or hatch. Collecting contour feathers from inactive nests allows females that failed early in incubation to be included and eliminates observer effects associated with visiting active nests (Bentzen et al. 2008b). Lastly, King Eider nests on the coastal plain occur at low densities, likely limiting nest sharing and feathers from multiple females occurring within one nest. Microsatellite genotyping of contour feathers to investigate patterns of breeding site fidelity in waterfowl has been successful (Fowler 2005), and this technique may significantly increase our ability to study site fidelity in species like King Eiders that nest in low densities and experience high nest failure.

We investigated local nest site fidelity of King Eiders using females marked through genotyping, and those marked with standard metal leg bands. Our objectives were to estimate return rates, determine whether females that had previously hatched a clutch (successful females) returned to the study areas at a higher rate, and to determine whether previously successful females nested closer to the previous nest than

unsuccessful females. We included marker type (genotyping and leg bands) in the analyses to examine differences in results based on methods. We predicted that high quality females, as indicated by previous success, would be more likely to be found at another nest in subsequent years and would remain close to previous successful locations within the study areas to take advantage of local nest site familiarity.

6.3. Methods

6.3.1. Study area

We studied King Eiders nesting at 2 sites on the arctic coastal plain of Alaska, one near Teshekpuk Lake (153°07'W, 70°25'N) and another ~150 km to the east within the Kuparuk oilfields (149°41'W, 70°27'N), 2002-2005 (Fig. 6.1). The Teshekpuk site was approximately 10 km south of the southeast shore of Teshekpuk Lake in the northeast planning area of the National Petroleum Reserve-Alaska (NPR-A) and experienced minimal human impact (i.e. no roads, communities, or development for petroleum extraction). The Kuparuk study site was between the Colville and Kuparuk river deltas, within a site developed for petroleum production, and had associated road networks and human activities. The study sites were characterized by numerous thaw lakes, ponds and wetland basins (Jorgenson et al. 2003). Wetland community types included wet sedge (*Carex* spp.) meadows, moist sedge-dwarf shrub (e.g. willow) meadows, and emergent *sedge* and pendant grass (*Arctophila fulva*) on the margins of lakes and ponds (Anderson et al. 1999). Dwarf willow was the dominant shrub and the main source of cover for nesting waterfowl (<40 cm in height). King Eider nest density ranged from 0 – 0.11

nests/ha at Teshekpuk and 0 – 0.16 nests/ha at Kuparuk within wetland basins. Approximately 38 nests were located at Teshekpuk and 35 nests at Kuparuk each year.

6.3.2. Field methods

We systematically searched wetland basins on foot for King Eider nests, beginning in mid-June at Teshekpuk (2001-2005) and Kuparuk (2004-2005). We searched a larger area at Kuparuk (Kuparuk, ~1500 ha; Teshekpuk, ~ 1000 ha) because of road access at that site. We marked nests with a tongue depressor placed 1 m away, in vegetation, to be concealed from potential nest predators. We recorded latitude and longitude of all King Eider nests using a hand-held Global Positioning System (GPS) unit. We monitored all nests once per week. After the initial nest visit, we avoided flushing hens from their nests. We designated a successful nest by presence of either eggshells with detached membranes (Girard 1939) or ducklings. If there were eggshells with no membranes, or if the entire clutch was absent, we considered the nest depredated. Nest contents (contour feathers, down, membranes and egg shell fragments) were collected after hatch or failure, dried, and stored at room temperature.

In conjunction with several other studies (Phillips 2005, Oppel 2008, Bentzen et al. 2008a), females were trapped on the nest using a drop or bow net during mid- to late-incubation at Teshekpuk (2002-2008) and Kuparuk (2002-2006). We banded (USGS aluminum bands) and collected head feathers from all captured birds. One female, and associated nest, occurred in both the banded sample of females and the genotyped sample. All aspects of the field work were approved by the University of Alaska

Fairbanks Institutional Animal Care and Use Committee (UAF IACUC 05-29-King Eider).

6.3.2. DNA sample preparation

Samples were extracted using a Qiagen DNeasy Blood & Tissue Kit protocol with the following modifications (Qiagen, Inc., Valencia, CA). Approximately a 1 cm portion of the feather base was diced up, placed in a 1.5 ml Eppendorf tube, and incubated in 180 µl ATL buffer with 30 µl Proteinase K (20 mg/ml) overnight at 55°C. The following day the samples were further macerated with a tissue grinder, an additional 30 µl of Proteinase K was added, and the samples were again incubated at 55°C overnight. The following day samples were extracted using the standard Qiagen animal tissue protocol (Qiagen, Inc., Valencia, CA) and eluted into 75 µl of dH_2O at 70°C. All amplifications were done using a 1 µl volume of these undiluted stocks.

6.3.2. Microsatellite methods

We screened 37 microsatellite primer pairs from a number of sources, for amplification and allelic variation using DNA obtained from ten eider blood samples. Ten of these loci produced strong amplifications and were polymorphic in King Eiders: Smo 6, 7, 8, 9, 13 developed for the common eider, *S. mollissima* (Paulus and Tiedemann 2003), Bcaµ1, Bcaµ11, Hhiµ5 (Buchholtz et al. 1998), Alaµ1 (Fields and Scribner 1997) and Sfi□9 (Libants et al. unpubl. data, GenBank accession number AF180499). The program API-CALC 1.0 was used to calculate the probability of identity to quantify the power of the chosen loci to resolve individuals (Ayres et al. 2004). The use of feathers as a DNA

source can increase the presence of genotyping errors, such as null alleles or large allele dropout. To access reproducibility and determine the extent of the presence of null alleles 15 samples were amplified in triplicate using the 10 loci. All loci exhibited amplifications of reproducible inambiguous peaks in the 150 opportunities examined (15 samples genotyped in triplicate for 10 markers).

Sample screening amplifications were performed using a PTC 100 thermal cycler (MJ Research, Waltham, MA). A total reaction volume of 10 µl was used with the following concentrations: 10 mM Tris-HCl at pH 8.3; 50 mM KCl; 0.001% gelatin; 3.0 mM $MgCl_2$; 100 µM for each of the dNTPs; 1X BSA (Alaµ1, Bcaµ1, Bcaµ11, Hhiµ5, Sfiµ9); 0.2 µm of each primer; 100 ng of template; and 1.5 U GoTag DNA polymerase (Promega, Madison, WI). The following parameters were used for amplifications: 3 min. denaturation at 93°C, followed by 35 cycles of 30 seconds at 93°C, annealing for 30 seconds at (47°C for Sfiµ9, 50 °C for Alaµ1, 52 °C for Smo 6, 7, 8, 9, and 13, and 55 °C for Bcaµ1, Bcaµ11, and Hhiµ5) and elongation at 72°C for 1 min. A final 10 min. period of elongation at 72°C followed the last cycle. Amplification products were analyzed on an ABI 3100 capillary DNA automated sequencer located in the Central Services Laboratory at Oregon State University, Corvallis, OR. ABI Genescan® analysis software was used to size fragments based on internal lane standard GeneScan 500 [Rox]. ABI Genotyper® software was used to score alleles accurately. The ten loci were examined using Micro-Checker (Oosterhout et al. 2004) to assess the presence of genotyping errors, such as nonamplified alleles, short allele dominance, and scoring of stutter peaks.

6.3.2. Data analyses

Probability of identity is the probability that two individuals drawn at random from a population will have the same genotype at multiple loci (P_{ID}), and is commonly used to determine whether genetic profiles consist of enough microsatellite loci to distinguish between individuals. As a conservative estimate, we calculated $P_{ID\text{-}sib}$ (probability of identity between siblings; GENALEX 6; Peakall and Smouse 2006) as an upper bound for the probability of observing identical multilocus genotypes from two individuals (Waits et al. 2001). Studies of population size estimation generally require a P_{ID} of less than 0.01 while forensic applications require a P_{ID} less than 0.001 (Mills et al. 2000, Waits et al. 2001). Genotypes that matched at all 10 loci were considered to be the same individual. We calculated observed (H_O) and expected heterozygosity (H_E), and deviations from Hardy-Weinberg equilibrium using GENALEX 6.

6.3.2.1. Local fidelity

We calculated return rates for the individuals identified through genotyping (hereafter referred to as genotyped) and for individuals identified by a standard leg band (banded) as the percentage of all marked individuals detected nesting in a subsequent year. We investigated whether banded females that previously hatched a clutch successfully had higher local fidelity. We refer to local fidelity as the probability that a female nesting in year *t* nested again in any year during the study on our study sites, and we detected that nest. Our estimate of fidelity is actually a product of survival, probability of returning to the breeding areas (study areas), and detection probability (see Anderson

et al. 1992). We use the term local fidelity with the understanding that it is confounded by mortality, emigration, and detection probability and should not be compared to estimates of fidelity measured at other scales. We excluded all females first banded in 2008 as no future detections were possible.

Our candidate model set examined the effects of nest success and site on nesting probability and included the models $\text{Fidelity}_{\text{success}}$, $\text{Fidelity}_{\text{site}}$, $\text{Fidelity}_{\text{success+ site}}$, and the null model. We used logistic regression (Allison 2000; SAS Institute, Cary, North Carolina) to fit models and used the second-order Akaike's Information Criterion (AIC_c) to identify the most parsimonious model and predict variable importance (Burnham and Anderson 2002). We calculated Akaike weight (w_i) for each model, representing probability of that model as being the best model in the set of candidate models (Burnham and Anderson 2002). We calculated the sum of model weights ($\sum w_i$) for each variable using weights of all models that contained that variable. We used model-averaged parameter estimates and unconditional standard errors averaged over all models that contained a variable to determine the importance of that variable within the candidate set of models. We calculated odds ratios from averaged parameter estimates that represented the increase in nesting probability for every unit increase in the predictor variable (Allison 2000).

6.3.2.2. Local movements

We measured distances between individuals' nests using ArcView Geographic Information System (Environmental Systems Research Institute, Redlands, California). In

order to avoid dependence between samples we randomly selected one pair of years per female. To determine if higher quality females remained closer to the previous nest (not necessarily consecutive years) we performed the following analyses. We used analysis of variance (ANOVA; PROC GLM, SAS Institute 1990) models to evaluate factors influencing distance moved between nests of banded females from 2002-2008 using 3 a priori candidate models with variables site and previous success ($Distance_{site}$, $Distance_{success}$, $Distance_{site+success}$). We examined residuals for normality (Shapiro-Wilk, $P > 0.05$). Distance moved was log transformed to meet the assumptions of ANOVA. We selected the best approximating models using AIC_c. Values reported in the results section are means ± SE.

6.4. Results

We collected contour feathers from 261 nests ($n_{Kuparuk} = 94$, $n_{Teshekpuk} = 167$) from 2001 to 2005. We detected 118 alleles at the ten typed loci with an average of 12 alleles per locus. The $P_{ID\text{-}sib}$ across the ten loci was < 0.001 which should be sufficient to distinguish between individuals even if all individuals are siblings (Table 6.1). One of three nests that had duplicate feather samples collected matched at all ten loci. Of the two duplicates that did not match, one differed at Bcaμ1, possibly due to allelic dropout, and the other at Smo7, Smo9, and Smo13. Additionally, one banded female captured on the nest in two years, and also present in the feather samples matched only at Bcaμ1. Only one of ten loci (SMO8) conformed to Hardy-Weinberg expectations (Table 6.1). Of the ten nests

where both the contour feathers and the female's head feathers were genotyped, only seven matched at all ten loci.

Based on the DNA typing, six females nested locally in more than one year and 148 were detected at only one nest from 2001 to 2005 (Teshekpuk) and 2004 and 2005 (Kuparuk). Of the females nesting from 2001 to 2004, 3.9% (95% CI = 0.8, 7.0) returned and nested at least once by 2005. The six genotyped females nesting in multiple years moved an average of 277 m between nests (± 75; not necessarily consecutive years). One female was detected at nests in 2002, 2003, and 2005, all within 600m.

We banded 44 females on the nest at Kuparuk from 2002 to 2006 of which five were recaptured in at least one other year. We banded 61 females at Teshekpuk from 2002 to 2008 of which nine were recaptured at least once. Females at Kuparuk had a return rate of 11.4% (95% CI = 2.0, 20.7) while females at Teshekpuk had a return rate of 14.8% (95% CI = 5.9, 23.7). Banded females moved an average of 331 m (± 119, n = 9; not necessarily consecutive years) at Teshekpuk, and 361m (± 66, n = 5) at Kuparuk. One female banded at Teshekpuk in 2006 was recaptured in 2007 and 2008; moving 126 m and 155 m between consecutive year nests.

6.4.1. Local fidelity

Banded females that previously hatched a clutch were not more likely to be found locally in subsequent years. The top candidate model ($Fidelity_{site}$; $AIC_c = 72.68$, AIC_c wt= 0.50) was 1.58 AIC_c units from the next best model ($Fidelity_{(.)}$; $AIC_c = 74.26$, AIC_c wt= 0.23),

the null model. Parameter results reflected the inadequacy of the variables included in the candidate model set with all model averaged odds ratios' 95% confidence intervals including 1 (β_{site}-hat= -0.83, 95% CI = -1.69 – 0.03; odds ratio = 0.44; $\beta_{success}$-hat = 0.08, 95% CI = -0.28 – 0.43; odds ratio = 1.08).

6.4.2. Local movements

The top model of the candidate model set describing distance moved between nests ($Distance_{site,success}$; AIC_c = -2.023, AIC_c wt= 0.44) was 0.07 AIC_c units from the next best model ($Distance_{success}$) and the top two models carried 87% of the weight. Model averaged parameter estimates (effects sizes, □-hat) indicated that successful females moved shorter distances between nests (261 ± 45, n = 11) than did females whose nests failed (636 ± 306m, n = 3). Distance moved between nests did not vary between Teshekpuk (331± 119m, n = 9) and Kuparuk (361 ± 66m, n = 5; $□_{site}$ = -0.40, 95% CI = -0.97 – 0.17)

6.5. Discussion

Estimates of return rates varied depending on the method used to identify individual females. Banded females had return rates of 13-17% while genotyped females appeared to return and nest only 4% of the time. Distance moved between nests was quite similar for females marked by the two methods (~300 m).

It is important to remember that band results are based on a small sample of females that were successful in incubating their nests at least through mid-incubation while genotyping results include females that failed very early. Unlike genotyped returns,

return rates for banded females are likely biased low due to nest failure prior to capture. Therefore, we would expect genotyping return rates to be higher than banding return rates, the opposite of what we found. The sample of females that are successful through late incubation may be of higher quality/more experienced females and thus could be expected to return in higher numbers. However, nest success is so low on the coastal plain (Bentzen et al. 2008b) that failure prior to capture would have had a larger impact on return rates than female quality.

Genotyping contour feathers deposited in nests did not appear to be a reliable method for determining site fidelity in King Eiders as a number of duplicate samples did not match. It is unclear exactly why genotyping didn't work; but possibilities including genotyping errors, errors by the field crew, and King Eider behavior. Genotyping errors that create 'ghost' eiders with incorrect genotypes are impossible to 'recapture' unless the same genotyping error occurs again. Allelic dropout is always a possibility with low quality DNA sources and one of the duplicate sample mis-matches could be attributed to this. However, allelic dropout in general did not seem to be a problem as we did not see short allele dominance at any locus. We had very high repeatability of the genotyping which should give us confidence that we are correctly identifying individuals. However, it is difficult to reconcile this high repeatability and the fact that the duplicate samples did not match.

Potentially, the non-matching duplicates could be due to errors by the field crew. We used GPS locations to identify nests, verifying the identity with the tongue depressor marker if there was any uncertainty. The GPS locations have an error of ~1m but King

Eiders (at Teshekpuk and Kuparuk) nested on average >400m apart (Bentzen et al. 2009) and the nests were usually easy to spot. However, on occasion nests were found within 2m from each other and there is a slim possibility of misidentifying nests. One of two duplicate samples that didn't match, was located on an island, making it even less likely that it was misidentified.

The samples were duplicated because two different crew members visited the nest separately and collected nest contents. The mismatched duplicates were collected between 7 and 28 days apart. The duplicate sample that did match was collected 32 days apart. The possibility exists that the nest bowl was reused during this period. However, King Eiders do not reuse nest bowls from previous years, and we have never observed a previously failed nest to be reused within a year (Rebecca Bentzen, unpubl. data). Also, these nests became 'available' in late June/early July when very few eiders are initiating egg laying (Bentzen et al. 2008b).

Since the nests are so widely dispersed it is quite unlikely that feather contamination would occur unless some females shared nests. We can rule out some sources of feather contamination through knowledge of King Eider breeding habits; males do not incubate, ducklings leave the nest prior to contour feather growth, and females do not bring nesting materials to the nest. If two females deposited feathers in the same nest, the contour feather used for genotyping could have come either female. Intraspecific brood parasitism is assumed for clutches with >7 eggs and was estimated at 16.2% in a high density island nesting population in northern Canada (Kellett and Alisauskas 1997). Only one nest at our sites had >7 eggs but it is possible that additional

nests had two females incubating although only one laid the eggs. Two King Eider females at the same nest have been observed, although it was uncertain if both were incubating (S. Oppel, University of Alaska Fairbanks, pers. comm). We tested a subset of samples using multiple feathers from each nest and feather contamination did not seem to be a problem. However, of 10 samples where we genotyped both the female's head feathers and the contours collected in her nest, only 7 matched. Again, we do not know for certain if this was due to feather contamination in the nest or to genotyping errors. Possibly multiple females incubating a single clutch is more prevalent than previously thought. If this is the case, it would certainly limit the usefulness of contours deposited within the nest.

The King Eiders in this dataset are likely to be related, possibly closely. Female common eiders exhibit high natal fidelity (Coulson 1984, Swennen 1990) and King Eiders may similarly nest close to related females. However, high relatedness should lead to multiple individuals being identified as one, not to surprisingly low return rates and mismatched duplicate samples. Relatedness may have led to the loci being out of Hardy-Weinberg equilibrium.

6.5.1. Banded female patterns of fidelity

We predicted that high quality females, as indicated by previous nesting success, would be more likely to be found at another nest in subsequent years. However, previous nest success did not influence return rates. Fidelity to the study areas over the duration of the study may have been influenced by a number of variables that we did not measure such

as female age, spring body condition, presence of predators in the area during nest site selection, spring snow and ice cover, and the scale of the study areas, both spatially and temporally. King Eiders rely on stored reserves during reproduction to a varying degree (Bentzen et al. 2008a, Oppel 2008) and may experience carry-over effects from the winter or spring that impact reproductive output (Alisauskas 2002, Lehikoinen et al. 2006, Drent et al. 2007). Nest success in any one year may not be an adequate predictor of female quality in a long lived species with relatively low annual reproduction. The low fidelity to the study areas during the years of the study may have been a result of females forgoing breeding in a number of years, possibly due to very poor spring condition (Coulson 1984). Spring body condition may be a factor of winter habitat conditions or conditions on the highly productive spring staging areas in the Eastern Chukchi and Beaufort Seas (Dunton et al. 2005, Phillips et al. 2007, Oppel et al. 2008). Periodic non-breeding has also been linked to low densities of lemmings and high densities of foxes (Palmer 1976, Sittler et al. 2000). We could only investigate indirect measures of female quality on fidelity and only for a relatively short period.

We hypothesized that previously successful females would nest near their previous nest to take advantage of local familiarity. Distance moved between nests was considerably lower for banded females that were successful in the previous year. This is similar to King Eiders nesting on islands at Karrak Lake, Northwest Territories (Kellett 1999), and spectacled eiders (*S. fischeri*) on the Yukon/Kuskokwim delta (Moran 2000) both of which moved shorter distances between nests after a successful nesting attempt.

King Eiders experience low nest success in northern Alaska (21-57%; Bentzen et al. 2008b) and feed during incubation while still maintaining very high incubation constancy (Bentzen et al. 2008a) suggesting that local familiarity of food resources and predators in the vicinity may be quite important. Improved feeding efficiency through familiarity of local food resources (see Anderson et al. 1992) is thought to be less important to waterfowl that rely more heavily on stored reserves. While King Eiders do rely heavily on stored reserves for maintenance needs during incubation, nutrients obtained on the breeding grounds are clearly important (Bentzen et al. 2008a).

In conclusion, we suggest that it is important that future studies using non-invasive genetic sampling with microsatellite genotyping not be undertaken unless a realistic method for checking the results exists. This could take the form of higher quality DNA collection (blood, muscle) for a subset of individuals, or, ideally, a subset of physically marked individuals to verify genotyping. Using a sample of physically banded females, we did not find strong effects of female quality, as measured by previous nest success, on local fidelity; suggesting that indirect measures of female quality in previous years do not adequately predict the probability that the female will return and nest within the next few years. However, nesting success in a previous year did influence nesting dispersal distance within the study area once she had returned. This suggests that the probability that a female will return to the breeding area is contingent on factors experienced during the winter and spring months in any one year but that local familiarity

of the breeding area influences nest site choice once the female is on the breeding grounds.

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6.7. Literature cited

Alisauskas, R. T. 2002. Arctic climate, spring nutrition, and recruitment in mid-continent lesser snow geese. – J. Wild. Manage. 66: 181-193.

Allison, P. D. 2000. Logistic regression using the SAS system: theory and application. SAS Institute, Inc., Cary, North Carolina.

Anderson, M. G., Rhymer, J. M. and Rohwer, F.C. 1992. Philopatry, dispersal, and the genetic structure of waterfowl populations. – In: Batt, B. D. Afton, A. D., Anderson, M. G., Ankney, C. D., Johnson, D. H., Kadlec, J. A. and Krapu, G. L.

(eds). Ecology and management of breeding waterfowl. University Minnesota Press, Minneapolis, pp. 365-395.

Anderson, B. A., Johnson, C. B., Cooper, B. A., Smith, L. N. and Stickney, A. A. 1999. Habitat associations of nesting spectacled eiders on the Arctic Coastal Plain of Alaska. . – In: Goudie, R. I., Peterson, M. R. and Robertson, G. J. (eds). Behavior and ecology of sea ducks. Canadian Wildlife Service Occasional Paper, Ottawa, Ontario, pp. 27-59.

Ayres, K. L., and A. D. J. Overall. 2004. API-CALC 1.0: a computer program for calculating the average probability of identity allowing for substructure, inbreeding and the presence of close relatives. Molecular Ecology Notes 4: 315-318.

Bentzen, R. L., Powell, A. N., Williams, T. D. and Kitaysky, A. S. 2008a. Characterizing the nutritional strategy of incubating king Eiders *Somateria spectabilis* in northern Alaska – J. Avian Biol. 39: 683-690.

Bentzen, R. L., Powell, A. N. and Suydam, R. S. 2008b. Factors influencing nesting success of king eiders on northern Alaska's coastal plain. – J. Wild. Manage. 72: 1781-1789.

Bentzen, R. L., Powell, A. N. and R. Suydam. 2009. Effects of concealment, seclusion, and nesting associations on nest site selection by king eiders. – J. Wild. Manage. 73:932-938.

Bluhms, P., Nichols, J. D. Hines, J. E. and Mednis, A. 2002. Sources of variation in survival and breeding site fidelity in three species of European ducks. – J. Anim. Ecol. 71: 438-450.

Brook, R. W. and Clark, R. G. 2002. Retention and effects of nasal markers and subcutaneously implanted radio transmitters on breeding female lesser scaup. – J. Field Orn. 73: 206-212.

Buchholz, W. G., Pearce, J. M., Pierson, B. J. and Scribner, K. T. 1998. Dinucleotide repeat polymorphisms in waterfowl (family Anatidae): characterization of a sex-linked (Z-specific) and 14 autosomal loci. – J. Anim. Genetics 29: 323-325.

Burnham, K. P. and Anderson, D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. – Springer-Verlag, New York.

Cotter, R. C., Dickson, D. L. and Gratto, C. J.1997. Breeding biology of the king eider in the western Canadian Arctic. In: Dickson, D. L. (ed). King and common eiders of the western Canadian Arctic. – Canadian Wildlife Service Occasional Paper 94, Ottawa, Ontaria, pp. 29-39.

Coulson, J. C. 1984. The population dynamics of the eider duck *Somateria mollissima* and evidence of extensive non-breeding by adult ducks. – Ibis 126: 525-543.

Dickson, D. L., Cotter, R. C., Hines, J. E. and Kay, M. F. 1997. Distribution and abundance of king eiders in the western Canadian Arctic. – In: Dickson D. L. (ed). King and common eiders of the western Canadian Arctic. Ottawa, Canada: Can. Wildl. Serv., pp. 29-39.

Drent, R., Eichhorn, G., Flagstad, A., Van der Graaf, A., Litvin, K. and Stahl, J. 2007. Migratory connectivity in Arctic geese: spring stopovers are the weak links in meeting targets for breeding. – J. Ornithol. 148: S501-S514.

Dunton, K. H., Goodall, J. L., Schonberg, S. V., Grebmeier, J. M. and Maidment, D. R. 2005. Multi-decadal synthesis of benthic–pelagic coupling in the western arctic: role of cross-shelf advective processes. – Deep-Sea Research II 52: 3462–3477.

Eggert, L. S., Patterson, G. and Maldonado, J. E. 2007. The Knysna elephants: a population study conducted using faecal DNA. – African J. Ecol. 46: 19-23.

Fickel, J. and Hohmann, U. 2006. A methodological approach for non-invasive sampling for population size estimates in wild boars (*Sus scrofa*). – Eur. J. Wild. Research 52: 28-33.

Fields, R. L. and Scribner, K. T. 1997. Isolation and characterization of novel waterfowl microsatellite loci: cross-species comparisons and research applications. – Mol. Ecol. 6: 199-202.

Fowler, A. C. 2005. Fine-scale spatial structuring in cackling Canada geese related to reproductive performance and breeding philopatry. – Anim. Behav. 69: 973-981.

Frantz, A. C., Pope, L. C., Carpenter, P. J., Roper, T. J., Wilson, G. J., Delahays, R. J. and Burke, T. 2003. Reliable microsatellite genotyping of the Eurasian badger (*Meles meles*) using faecal DNA. – Mol. Ecol. 12: 1649-1661.

Girard, G. L. 1939. Notes on the life history of the shoveler. – Trans. North Am. Wildl. Conf. 4:364-371.

Gratto-Trevor, C. L., Johnson, V. H. and Pepper, S. T. 1998. Changes in shorebird and eider abundance in the Rasmussen Lowlands, NWT. – Wilson Bull. 110: 316-325.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. – Anim. Behav. 28: 1140-1162.

Jorgenson, M. T., Roth, J. E., Emers, M., Schlenter, S. F., Swanson, D. K., Pullman, E. R., Mitchell, J. S. and Stickney, A. A. 2003. An ecological land survey in the

northeast planning area of the National Petroleum Reserve-Alaska, 2002. ABR, Inc., Fairbanks, Alaska.

Kellett, D. K. 1999. Causes and consequences of variation in nest success of king eiders (*Somateria spectabilis*) at Karrak Lake, Northwest Territories. – M.Sc. Thesis, University of Saskatchewan, Saskatoon.

Kellett, D. K, Alisauskas, R. T. and Mehl, K. R. 2003. Nest-site selection, interspecific associations, and nest success of king eiders. – Condor 105: 373-378.

Kellett, D. K., and Alisauskas, R.T. 1997. Breeding biology of king eiders nesting on Karrak Lake, Northwest Territories. – Arctic 50: 47-54.

Lack, D. 1954. The natural regulation of animal numbers. – Claredon Press, Oxford.

Lamothe, P. 1973. Biology of the king eider (*Somateria spectabilis*) in a freshwater breeding area on Bathurst Island, N.W.T. – M.Sc. Thesis, University of Alberta, Edmonton, Alberta.

Lehikoinen, A., Kilpi, M. and Öst, M. 2006. Winter climate affects subsequent breeding success of common eiders. – Global Change Biol. 12:1355-1365.

Mehl, K. R., Alisauskas, R. T., Hobson, K. A. and Kellett, D. K. 2004. To winter east or west? Heterogeneity in winter philopatry in a central-arctic population of king eiders. – Condor 106: 241-251.

Mills, L., Citta, J., Lair, K., Shwartz, M. and Tallmon, D. 2000. Estimating animal abundance using non-invasive DNA sampling: promise and pitfalls. – Ecol. Appl. 10: 283-294.

Moran, L. M. 2000. Spatial-temporal variation in reproduction and site fidelity of spectacled eiders on the Yukon-Kuskokwim Delta, Alaska. – M.Sc. Thesis, University of Alaska, Fairbanks.

Mowat, G. and Strobeck, C. 2000. Estimating population size of grizzly bears using hair capture, DNA profiling, and mark-recapture analysis. – J. Wild. Manage. 64: 183-193.

Oppel, S. 2008. King eider migration and seasonal interactions at the individual level. – Ph.D. Dissertation, University of Alaska Fairbanks, Fairbanks, Alaska.

Oppel, S., Powell, A. N. and Dickson, D. L. 2008. Timing and distance of king eider migration and winter movements. – Condor 110: 296-305.

Oosterhout, C. V., Hutchinson, W. F., Willis, D. P. M. and Shipley, P. 2004. MICRO-CHECKER: software for identifying and correcting genotyping errors in microsatellite data. Molecular Ecology Notes 4: 535-538.

Palmer, R. S. 1976. Handbook of North American birds. Vol. 3, Yale Univ. Press, New Haven, Conneticut.

Palsbøll, P.J., Allen, J., Bérubé, M., Clapham, P. J., Feddersen, T. P., Hammond, P. S., Hudson, R. R., Jørgensen, H., Katona, S., Larsen, A. H., Larsen, F., Lien, J., Mattila, D. K., Sigurjønsson, J., Sears, R., Smith, T., Sponer, R., Stevick, P. and Øien, N. 1997. Genetic tagging of humpback whales. – Nature 388: 767-769.

Paulus K. B. and Tiedemann, R. 2003. Ten polymorphic autosomal microsatellite loci for the Eider duck *Somateria mollissima* and their cross-species applicability among waterfowl species (Anatidae). – Mol. Ecol. 3:250-252.

Peakall, R. and Smouse P.E. 2006. GENALEX 6: genetic analysis in Excel. Population genetic software for teaching and research. – Mol. Ecol. Notes 6: 288-295.

Pearce, J. M., Fields, R. L. and Scribner, K. T. 1997. Nest materials as a source of genetic data for avian ecological studies. – J. Field Ornithol.68: 471-481.

Phillips, L. M. 2005. Migration Ecology and Distribution of King Eiders. – M.Sc. Thesis University of Alaska Fairbanks, Fairbanks, Alaska.

Phillips, L. M. and Powell, A. N. 2006. Evidence for wing molt and breeding site fidelity in king eiders. – Waterbirds 29: 148-153.

Phillips, L. M., Powell, A., Taylor, E. J. and Rexstad, E. A. 2007. Use of the Beaufort Sea by king eiders nesting on the North Slope of Alaska. – J. Wild. Manage. 71: 1892-1899.

Regehr, H. M. and Rodway, M. S. 2003. Evaluation of nasal discs and colored leg bands as markers for Harlequin Ducks. – J. Field Ornithol. 74: 129-135.

SAS Institute. 1990. SAS/STAT user's guide. Version 6, 4th ed. SAS Institute, Cary, NC.

Sittler, B., Gilg, O. and Berg, T. B. 2000. Low abundance of king eider nests during low lemming years in northeast Greenland. – Arctic 53: 53-60.

Suydam, R. S., Dickson, D. L., Fadely, J. B. and Quakenbush, L. T. 2000. Population declines of king and common eiders of the Beaufort Sea. – Condor 102: 219-222.

Swennen, C. 1990. Dispersal and migratory movements of eiders Somateria mollissima breeding in the Netherlands. – Ornis Scand. 21: 17-27.

Taberlet, P., Camarra, J-J. and Griffin, S. 1997. Non-invasive genetic tracking of the endangered Pyrenean brown bear population. – Mol. Ecol. 6: 869-876.

Waits, L. P., Luikart, G., and Taberlet, P. 2001. Estimating the probability of identity among genotypes in natural populations: cautions and guidelines. – Mol. Ecol. 10: 249-256.

Table 6.1. Number of alleles scored, estimated heterozygosity (H_E), observed heterozygosity (H_O), probability of fit to Hardy-Weinberg equilibrium (HWE), and probability of identity (P_{ID}) for 10 King Eider microsatellite loci. Analyzed for 261 females nesting at Teshekpuk and Kuparuk, Alaska, 2001-2005, ranked by P_{ID}/locus.

Locus	Number of alleles scored	H_E	H_O	HWE	P_{ID}/locus[a]	$P_{ID\text{-}sib}$/locus[b]	$P_{ID\text{-}sib\text{-}prod}$/locus[c]
Smo6	21	0.90	0.87	<0.001	0.017	0.302	0.302
Smo9	16	0.83	0.52	<0.001	0.051	0.350	0.106
Sfiμ9	9	0.74	0.66	<0.001	0.096	0.403	0.043
Bcaμ11	9	0.74	0.67	<0.001	0.104	0.405	0.017
Alaμ1	12	0.68	0.52	<0.001	0.133	0.443	0.008
Smo13	12	0.63	0.53	<0.001	0.159	0.475	0.004
Smo7	9	0.66	0.59	<0.001	0.173	0.464	0.002
Hhiμ5	10	0.58	0.37	<0.001	0.223	0.516	0.001
Bcaμ1	7	0.40	0.26	<0.001	0.385	0.647	0.001
Smo8	13	0.39	0.39	0.999	0.389	0.654	0.000

[a]Probability of identity for individual loci

[b]Probability of identity assuming all individuals are siblings

[c]Probability of identity across loci by sequentially multiplying the P_{ID} value over loci assuming all individuals are siblings.

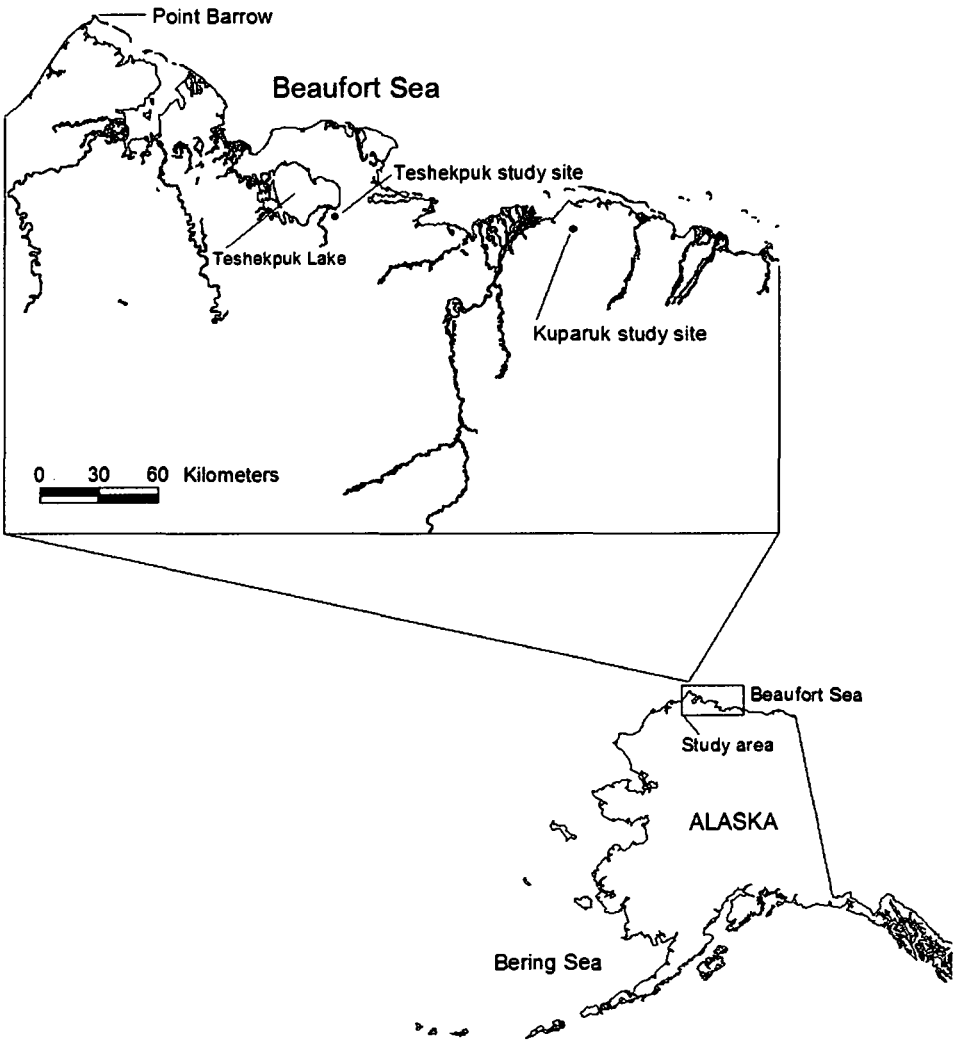

Figure 6.1. Locations of Kuparuk and Teshekpuk study areas (2002-2005) on the coastal plain of northern Alaska, USA.

7. CONCLUSIONS

I hypothesized that there were four main driving factors that influence nest survival of tundra-nesting waterfowl through a variety of pathways: forage availability on the breeding grounds, female body condition, and avian and mammalian predation pressure. These drivers are mediated by the nesting strategy used by the species in question, I found that King Eiders (*Somateria spectabilis*) nesting in northern Alaska fit the model with some modifications.

Incubation constancy is predicted to be the main mediating life history characteristic for variation in both forage availability and body condition (Fig. 7.1). However, I did not detect an effect of incubation constancy on nest survival at an individual level, possibly eliminating the pathway by which forage availability and body condition influence nesting success. I suspect that the lack of a detectable effect was due either to low power due to lack of variation in incubation constancy or to no effect during periods of high fox predation. Remote cameras (R. L. Bentzen, unpubl. data) showed that King Eider eggs were only lost to avian predators when the female was absent from the nest, suggesting they should benefit from high incubation constancy in the presence of avian predators and supporting a link between incubation constancy and nest success. However, in the presence of high fox predation, any effect of incubation constancy on King Eider nest success may be masked. Accordingly, the relationship between incubation constancy and nesting success may only be measureable in years or at locations with low fox predation pressure. Unfortunately, I did not encounter such conditions during my study and as such I don't believe my data can be used to reject the

presence of this relationship. Therefore the link between incubation constancy and nest survival remains in the conceptual model (Fig. 7.1) although clearly measurement of this relationship deserves further study.

Given limitations of my study and resulting data, I was unable to investigate some pathways through which incubation constancy may influence or be influenced by the other life history characteristics. I was unable to verify the effect of weight loss on abandonment due to low numbers of abandoning females. This may be difficult to determine under natural conditions as females are adapted to avoid this situation (Criscuolo et al. 2002). Measurement of such thresholds in body condition will likely require manipulative studies. I did not detect a link between incubation constancy and forage availability as inferred by plasma concentrations of lipid and protein metabolites (Chapter 2), possibly due to a lack of variability and small sample sizes. Lastly, I was unable to investigate a link between incubation constancy and increased number of avian predators in the area due to my study design. However, incubation constancy was positively correlated with body mass during incubation (Chapter 1) confirming its link to weight loss (Fig. 7.1).

Avian and mammalian predation pressure may influence King Eider nest survival directly or be mediated by nest site selection and incubation constancy. There was no evidence that King Eiders choose or benefit from nesting associations (Chapter 4) and I removed nesting associations from the model invalidating the influence of associations on incubation constancy. Additionally, there was no indication that nest site selection

influenced constancy, although I only investigated the difference between island and mainland nests (Chapter 1). Females did select for concealed and secluded nest sites although I only detected a benefit from concealed nests (Chapter 4; Fig. 7.1).

King Eiders nesting at two sites (Teshekpuk and Kuparuk) on Alaska's coastal plain differed in a number of reproductive parameters, suggesting that nesting strategies and perhaps selection pressures differed between them. In comparison with the Teshekpuk study area, Kuparuk varied in a number of ways: it was within an area developed for oil and gas extraction and may have had higher densities of predators due to anthropogenic food sources (Eberhardt et al. 1982, Truett et al. 1997, Burgess 2000), wetland basins tended to be larger and farther apart (Chapter 4), and the ambient temperature was cooler (Chapter 1). I evaluated the difference in nesting strategies using the predictions outlined in the introduction to this dissertation to try and determine how selective forces varied between the two sites.

Given the conceptual model for King Eiders (Fig. 7.1), the associated predictions could be modified from the general waterfowl model. I determined that females arrived to the breeding grounds at similar body mass at both sites (Chapter 1), therefore I did not consider those predictions associated with variation in body condition. Female King Eiders fed during incubation (Chapter 2) and egg laying (Oppel 2008) and food intake varied between sites (Chapter 2); therefore I only considered predictions concerning difference in food availability between sites. Lastly, I removed predictions associated with nesting associations because I found no indication that King Eiders associated with

aggressive nest defenders. The modified table of predictions (Tables 7.1 and 7.2) now consists of four hypothesized selective differences between sites (equal fox and avian predation and varying forage availability, equal avian predation and varying fox predation and forage availability, etc.) each with five associated predictions.

The predictions have a number of assumptions that I evaluated. Degree of concealment available did not differ between sites (Chapter 4). However, islands at Teshekpuk may have been more secluded than those at Kuparuk (Kuparuk average distance to mainland = 56.7 ± 95.6 m, average water depth = 37.3 ± 32.6 cm; Teshekpuk, average distance to mainland = 153.6 ± 202.8 m, average water depth = 28.5 ± 25.5 cm; Chapter 4), possibly violating the assumption that availability of secluded sites did not differ between sites. However, the difference in seclusion was largely due to distances from islands to mainland, and it is unknown whether foxes are deterred by having to wade long distances through very shallow water.

King Eiders breeding on Alaska's coastal plain matched the predictions for more available forage at Kuparuk and no differences in either avian or mammalian predation pressure between sites. King Eiders at Kuparuk had higher nest survival and incubation constancy, began and ended incubation at a similar mass, and selected similar nests when compared to females at Teshekpuk (Table 7.3). It is somewhat surprising that habitat quality appeared to be higher at Kuparuk than Teshekpuk since King Eider breeding pair densities have been consistently lower at Kuparuk from 1993-2006 (Larned et al. 2006). However, King Eider nest density was fairly similar between sites (Teshekpuk, 0 – 0.11

nests/ha; Kuparuk 0 – 0.16 nests/ha) within wetland basins and perhaps the density differences were due to the proportion of the landscape that is actually available nest sites. Further, I did not measure all life history characteristics associated with fitness and its possible that higher success during nesting may be offset by lower success during brood rearing.

Female King Eiders at both sites used the same wintering and spring staging areas (Oppel et al. 2008), and arrived on the breeding grounds in similar condition (Chapter 1). However, the nutritional strategy of King Eiders on the breeding grounds appeared to vary between the two sites, further supporting the prediction that forage availability was higher at Kuparuk. Females at Kuparuk invested more exogenous resources into egg production (Oppel 2008), used more fat reserves during incubation, and had higher food intake rates while maintaining higher incubation constancy (Table 7.3). This would seem to suggest that females at Kuparuk managed to compensate for more metabolically demanding conditions during incubation (cooler ambient temperatures) by higher food intake rates made possible by higher food availability (Chapter 2). Females at Kuparuk may use more exogenous resources for egg formation in order to retain body reserves for incubation (Bond et al. 2007, Gorman et al. 2008, Oppel 2008). It appears King Eiders attempt to achieve an optimal rate of mass loss through modification of their incubation behavior in response to endogenous nutrient reserves available for maintenance needs and environmental conditions similar to what has been shown for common eiders (Criscuolo et al. 2002).

Predation was the largest cause of nest failure for King Eiders (Kellett et al. 2003, R.L. Bentzen, unpublished data). I observed arctic fox (*Alopex lagopus*), glaucous gulls (*L. hyperboreus*), and parasitic (*S. parasiticus*) and long-tailed (*S. longicaudus*) jaegers depredating nests (Chapter 3). However, predation pressure did not seem to have caused study site differences as predicted by the model. It is important to note that I may be unable to differentiate between sites using this model and prediction where the effects of avian and mammalian predation obscure each other. For example, high avian predation pressure may eliminate any visible benefits to seclusion despite higher fox predation pressure. Additionally, predator density may not translate directly into predation probability if there is abundant alternative prey. High predator numbers in the oilfields are assumed to harm tundra-nesting birds, but King Eiders at Kuparuk may actually benefit from oil and gas infrastructure if egg predators are substantially subsidized by anthropogenic food sources. Garbage disposal has drastically improved in the oilfields over the past decades but there are numerous instances of dumpsters left open, lunch sacks stored in open pickup beds, and feeding by oilfield personnel (Dick Shideler, Alaska Department of Fish and Game, pers. comm). While is important to note that these are rule infractions within the oilfields, there are clearly food sources available to various predators. Future management should take into consideration the possibility of high densities of predators suddenly impacting tundra-nesting waterfowl if alternative food sources are removed.

I assumed that islands provide some protection from mammalian predators and that the degree of protection available would not vary between sites. However, I did not find any preference for more isolated islands, potentially due to a lack of truly isolated islands on the coastal plain, and females did not experience higher nest survival on islands (Chapters 3 and 4). King Eiders nesting in areas with only shallow-water tundra ponds (which characterizes much of their circumpolar range) may not have had a viable option for secluded nesting. Without truly secluded nest sites, low densities of foxes or abundant alternative prey leading to decreased predation pressure by foxes may be required for successful breeding (Bêty et al. 2001). If there are no truly secluded sites then selection for, and benefits from, seclusion will not accurately reflect mammalian predation pressure. It is also possible that the benefits of seclusion may be most pronounced at more moderate levels of predation than encountered during my study. That is, islands may not provide protection if mammalian predation is very high; if foxes are desperate to find waterfowl eggs, they may expend the extra effort required to access even relatively secluded islands.

I removed nesting associations as a parameter of interest when trying to differentiate between selective forces differing between Kuparuk and Teshekpuk because I found no evidence that King Eiders selected nest sites near glaucous gulls (Chapter 4) or that nest survival was affected by proximity to glaucous gull nests (R. L. Bentzen, unpublished data). Nesting associations can be difficult to detect; they can be confounded with habitat associations where both species select the same nest habitat, or

they may be serendipitous in that both waterfowl and their associates may nest at high numbers or experience high nest success in years when an alternative prey, such as lemmings, are abundant. During our study, lemming populations were low and invariant (R. L. Bentzen, personal observation), possibly limiting our ability to detect beneficial nesting associations (Bêty et al. 2001). The ability of nesting associations to reflect avian predation probability may depend upon the avian predators in question. For example, eiders may choose to associate with territorial pairs of gulls to avoid itinerant groups of gulls (Reed et al. 2007). Therefore an increase in the number of itinerant gulls may have a different result than an increase in the number of resident breeding gulls. If nesting associations are present in the system in question, it will be important to determine how any benefits accrue.

In summary, nest survival, use of endogenous reserves and food intake rates during incubation, and incubation constancy were higher at Kuparuk, while nest site selection, mass loss during incubation, and spring body condition did not vary between sites. This suggests that females at Kuparuk were compensating for more metabolically demanding conditions by increasing food intake, made possible by higher food availability. It appeared that the dynamics of predation pressure between the sites did not differ; females selected similar nests and nest success did not vary by habitat type between the two sites. To more fully investigate the evolution of nesting strategies, a study could be designed with sufficient power to detect the impact of body mass, predation pressure, and forage availability on incubation constancy, food intake, and nest

success at an individual level. Unfortunately, this is nearly impossible given the low nest density, difficulty in capture, and high early nest failure of most tundra-nesting ducks.

In conclusion, I presented a conceptual model for selective forces influencing nesting strategies of tundra nesting waterfowl in the introduction of my dissertation. The model is a theoretical representation of the links, at an individual level, between various reproductive parameters and the main factors influencing them (available forage, body condition, and predation pressure) which can explain patterns observed at a site level. A number of these links have been shown and are generally accepted by the scientific community, although not specifically for King Eiders. As with all correlative studies, I cannot prove that relationships exist, but to some extent I can reject relationships that don't. The resulting model is considerably simpler than originally envisioned. Modifying the conceptual model and associated predictions allowed me to understand and interpret reproductive patterns of King Eiders observed in the field.

Interpretation of my results in the context of selection pressure requires caution. Realizing that natural selection removes heritable variation from a population, then traits under strong selection pressure would be expected to show little variation making relationships hard to detect. The relationship between incubation constancy and nesting success fit this scenario. In other cases, I found substantial variation but still found no relationship, implying that either selection pressure is minimal, or environmental heterogeneity maintains variation within the population. Although questions concerning the nesting strategies of King Eider remain, I believe that the conceptual model was a

valid approach to identifying selective forces impacting nesting strategies and applicable to tundra nesting waterfowl in general. Investigating patterns and inferring from those patterns can only suggest how selective pressures are influencing nesting strategies, not conclude definitely, but through replication at other locations or across other species, we can begin to accrue evidence that supports one conclusion or another.

7.1. Literature Cited

Bêty, J., G. Gauthier, J. –F. Giroux, and E. Korpimäki. 2001. Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. Oikos 93:388-400.

Bond, J., D. Esler, and K. Hobson. 2007. Isotopic evidence for sources of nutrients allocated to clutch formation by Harlequin Ducks. Condor 109:698–704.

Burgess, R. M. 2000. Arctic fox. Pages 159-178 *in*: J. C. Truett and Johnson, S. R., editors. The natural history of an arctic oil field: Development and the biota. Academic Press, San Diego, USA.

Criscuolo, F., Gabrielsen, G. W., Gendner, J. –P. and Le Maho, Y. 2002. Body mass regulation during incubation in female common eiders *Somateria mollissima.* Journal of Avian Biology 33:83-88.

Eberhardt, L. E., W. C. Hanson, J. L. Bengtson, R. A. Garrott, and E. E. Hanson. 1982. Arctic fox home range characteristics in an oil-development area. Journal of Wildlife Management 46:183-190.

Gorman, K. B., D. Esler, P. L. Flint, and T. D. Williams. 2008. Nutrient reserve dynamics during egg production by female Greater Scaup (*Aythya marila*): relationships with timing of reproduction. Auk 125:384-394.

Kellett, D. K., R. T. Alisauskas, and K. R. Mehl. 2003. Nest-site selection, interspecific associations, and nest success of king eiders. Condor 105: 373-378.

Larned, W., R. Stehn, and R. Platte. 2006. Eider breeding population survey arctic coastal plain, Alaska 2006. U.S. Fish and Wildlife unpublished report, Anchorage, Alaska.

Oppel, S. 2008. King eider migration and seasonal interactions at the individual level. Ph.D. Dissertation, University of Alaska Fairbanks, Fairbanks, USA.

Oppel, S., A. N. Powell, and L. Dickson. 2008. Timing and distance of king eider migration and winter movements. Condor 110: 296-305.

Reed, J. A., D. L. Lacroix, and P. L. Flint. 2007. Depredation of Common Eider, Somateria mollissima, nests on a central Beaufort Sea barrier island: a case where no one wins. Canadian Field-Naturalist 121: 308-312.

Truett, J. C., M. E. Miller, and K. Kertell. 1997. Effects of arctic Alaska oil development on brant and snow geese. Arctic 50:138-146.

Table 7.1. Predicted difference in reproductive parameters of tundra-nesting waterfowl with equal fox predation pressure and female body condition on arrival at the breeding grounds and varying avian predation pressure relative to a nesting area with lower available forage.

	More available forage	Parameters
Equal avian predation pressure	Higher	Incubation constancy
	Higher	Nest success
	Choose similar nests	Seclusion
	Choose similar nests	Concealment
	Equal	Weight loss
Higher avian predation pressure	Higher	Incubation constancy
	Equal	Nest success
	Choose similar nests	Seclusion
	Choose and benefit from concealment	Concealment
	Equal	Weight loss

Table 7.2. Predicted difference in reproductive parameters of tundra-nesting waterfowl with equal female body condition on arrival at the breeding grounds and varying avian predation pressure relative to a nesting area with lower available forage and fox predation pressure.

	More available forage	Parameters
Equal avian predation pressure	Higher	Incubation constancy
	Lower	Nest success
	Choose and benefit from seclusion	Seclusion
	Choose similar nests	Concealment
	Equal	Weight loss
Higher avian predation pressure	Higher	Incubation constancy
	Lower	Nest success
	Choose and benefit from seclusion	Seclusion
	Choose and benefit from concealment	Concealment
	Equal	Weight loss

Table 7.3. Estimates of reproductive parameters of king eiders nesting at two sites, Teshekpuk and Kuparuk, Alaska, 2002-2006.

Parameters	Teshekpuk	Kuparuk
Incubation constancy[a]	95-99%	98-99%
Nest survival[b]	0.27-0.40	0.21-0.57
Seclusion[b]	No benefit	No benefit
Concealment[b]	Nest success higher at concealed nests in the presence of observers[c]	Nest success higher at concealed nests in the presence of observers[c]
Nesting associations[d]	None	None
Spring body mass[a]	1541-1805 g	1616-1760 g
Weight loss[e]	18.4 ± 3.6 g day^{-1}	18.4 ± 3.6 g day^{-1}
Food intake (triglyceride levels)[e]	0.52 ± 0.09 mmol/l	0.86 ± 0.07 mmol/l
Reliance on lipid reserves (β-hydroxybutyrate levels)[e]	2.05 ± 0.31 mmol/l	3.08 ± 0.22 mmol/l

[a]Chapter 1

[b]Chapter 3

[c]Benefit of concealment does not differ between sites

[d]Associations with aggressive nest defenders, Chapter 4

[e]Chapter 2

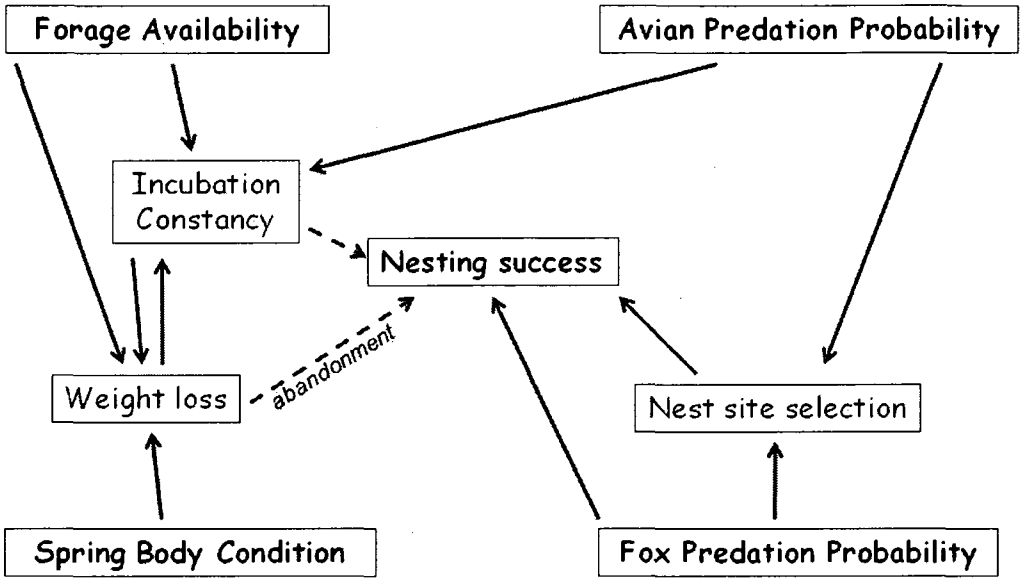

Figure 7.1. Conceptual model of the major driving factors and mediating life history characteristics influencing nest survival for King Eiders on Alaska's coastal plain.